VOL. I, NO. 4 OCTOBER, 1926

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THE QUARTERLY REVIEW
of BIOLOGY

FETAL GROWTH OF MAN AND OTHER PRIMATES

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I. INTRODUCTION

WHEN human growth is divided into an embryonic, a fetal, and a post-natal period, it is found that our knowledge in regard to the first and last parts is far more advanced than that of the middle or fetal period. Of all biological sciences embryology and physical anthropology have contributed the largest shares to the literature on human growth. The physiology and the histology of growth have been investigated much less and not until in comparatively recent years, the latter for instance by Levi (1925), the former by Friendenthal (1914). Comparative studies on the growth of different animals have been undertaken for but few and special purposes and no comprehensive paper on this promising problem is available as yet. In short, it can be stated that of the multitutde of questions, arising from the study of growth, a large proportion has up to the present time either not been answered at all or only in a tentative and incomplete manner.

This review is restricted almost entirely to observations from the field of physical anthropology and places main emphasis on the period of growth extending from the time the embryo has gained a definitely human form to birth. In other words, the following discussion will deal principally with those ontogenetic changes in body size and proportions which take place during that phase of development which links the period properly assigned to embryology with that covered by the enormous literature on growth in children (Baldwin (1921) has collected 911 titles pertaining to the growth of man from birth to maturity). Conditions in juveniles and adults are mentioned in this paper merely in order to indicate the general trend of growth changes during life after birth, and to compare certain features of fetal development with those at later stages of growth.

Literature

As mentioned before, the literature on human fetal growth is, relatively speaking, not very extensive. The majority of the papers have a very limited scope, dealing only with the weight and some

human fetus is of the 4th month, the gorilla and the gibbon fetus correspond in development to the human fetus, but the chimpanzee and the orang fetus are slightly more advanced in their growth. The figures for chimpanzee and gorilla have been constructed from measurements and photographs in the literature.

few main dimensions of the fetus. Detailed investigations on fetal body proportions are with few exceptions based upon insufficient material, from a study of which it has been rarely possible to arrive at the typical, representative conditions. Individual variations are fully as frequent and pronounced before birth as in later stages of growth, as shown, for instance, by Fischel (1896) and Mehnert (1896) for vertebrates in general and by the author (1926 c) for man in particular. To examine large numbers of individuals is, therefore, as essential for conclusions on prenatal development, as it was always deemed absolutely necessary in work on the growth of children.

Little could be gained here by attempting an exhaustive review of the literature on fetal growth in man. This would require an undue amount of space, in which to enumerate and analyze the many discrepancies—often due to inaccurate technique—in the results of the older investigators. Therefore, only some of the more important papers will be mentioned in this introduction, and reference to others will be made later on in connection with the particular problems on which they bear. The main part of this paper will be devoted to a presentation of final facts and of recent observations, while the varying and more or less hypothetical interpretations of these findings will be assigned a subordinate rôle.

The first problem of prenatal growth is the correlation between age and size of the developing organism. Data on this serve also in another fundamental problem, namely in the calculation of the rate of growth in the different periods of intrauterine life. Of the authors who have worked along these lines the following may be mentioned: Hecker (1866), Ahlfeld (1871), Fesser (1873), Calderini (1875), Henning (1879), Toldt (1879), Hamy (1880), Preyer (1885), Faucon (1897), Daffner (1902), Loisel (1903), Michaelis (1906), Roberts (1906), Tuttle (1908), Stratz (1909 a & b), Jackson (1909), Mall (1910 & 1918), Zangemeister (1911), Weissenberg (1911), Friedenthal (1911), Meyer (1914 & 1915), and Streeter (1920). Very extensive and reliable data are contained in the paper by the last named author and it is upon this paper that the writer has based the age estimation of his material.

A number of attempts have been made, chiefly by Noback (1922), Scammon and Calkins (1923), and Arey (1925), to reduce various phases of fetal growth to mathematical formulae by introducing certain constants. In view of the above mentioned high variability during fetal life and for certain reasons, to be referred to later on, such formulae can represent only a rough approximation to the actual and complicated conditions of growth.

The fetal growth of the head has been studied particularly from the obstetrical point of view, as for instance by Legou (1903), León (1912), and Calkins (1922). Detailed investigations on the growth before birth of the limbs alone have been made chiefly by Burtscher (1877), Mendes Corréa (1919), and Reicher (1925). A variety of measurements, covering all parts of the fetal body, have been published by Retzius (1904), who based his studies on a total of 87 specimens, by Reicher (1923), who had a series comprising 366 fetuses, and by the writer (1922 & 1923 b), who has examined a series of 623 fetuses.

Fetuses of different human races

Unfortunately there are as yet but few publications on fetuses of races other than the white. Friedenthal has described the fetus of a Papua (1913) and one of a negro (1914). Some few data on seven fetuses

of the latter race have been published by Hamy (1881). The writer (1920) has studied the prenatal development of the nose on a large series of negroes and on some Filipinos, American Indians, and Japanese, and in a later paper (1923 b) he gave a preliminary report on the general body proportions of 168 negro fetuses. Three recent papers deal with Japanese fetuses: Kudô (1923) gives data on the viscera of 111 specimens, Akiba (1924) measured certain proportions, particularly in regard to the limbs, on 160 fetuses, and Nishizuka (1925), in an excellent study on the development of the bones in the extremities of the Japanese (70 specimens of prenatal stages), lists a few fetal proportions.

Fetuses of apes and monkeys

The changes during growth in the size and proportions of the body, when studied in man alone, can mostly go little beyond a mere recording of the bare facts and allow but few conclusions as to the probable reasons underlying the changes. Many of the reasons, however, are suggested by comparing human growth with that in other animals, particularly other primates. For such comparative growth studies relatively little help is found in the literature. Not only have rather few data on fetuses of monkeys or apes been recorded, but the varying technique, employed by the different authors in measuring their material, renders exact comparison almost impossible. Some embryos and fetuses of various primates have been described (mostly with good illustrations, but with few, if any, measurements) by Kollmann (1892 a & b), Selenka (1892, 1899, & 1903), Wiedersheim (1901), Frédéric (1905), Keibel (1906 & 1911), and Bluntschli (1913). Data on other specimens, including some detailed measurements, have been published by Trinchese (1870) for an orang-utan fetus, by Deniker (1884 & 1885) for a gorilla and a gibbon fetus, by Toldt (1903) for two macaque fetuses, by Duckworth (1904) for a gorilla fetus, by Schwalbe (1911) for 4 orang fetuses, 23 gibbon and siamang fetuses, and 67 Asiatic monkey fetuses, by Friedenthal (1914) for two chimpanzee fetuses, and by the writer (1921 b) for two howler monkey fetuses, (1924 a) for three Colobus monkey fetuses, and (1924 b) for 5 anthropoid fetuses, 12 gibbon and siamang fetuses, 25 fetuses of Old World monkeys and 24 fetuses of American monkeys. In addition to these prenatal stages use was made of 109 infantile, juvenile, and adult monkeys and apes. Detailed information on the different species and on all the measurements and observations obtained from this material will soon be published elsewhere. The species names, used in this paper, are according to Elliot (1913).

Recapitulation theory

It is evident from these references to previous work on the development of different human races and of the various monkeys and apes, that no complete picture of fetal growth in primates can be given as yet, since only for the white race of man are there anywhere nearly sufficient data available. However, these comparative studies have progressed far enough to establish at least some of the outlines for this new chapter of science, in which embryology, physical anthropology, and primatology coöperate and really overlap. These outlines promise to be very helpful for our understanding of the many widely diverging specializations in different primates, including man. It will be shown later on that a great many human racial differences are already apparent in the fetus. This is, of course, not restricted to man, but holds true also

in regard to other mammals. For instance, Lönnberg (1917) has shown that in elephant fetuses the racial characteristics are very conspicuous, and this comparatively early since one specimen of *Elephas africanus cottoni* Lydekker had a crown-rump length of only 305 mm. The writer found some of the distinguishing features of certain breeds of dogs well defined in fetuses. Most of the peculiarities of the different monkeys and apes are clearly indicated before birth. However, racial differences, as well as the distinguishing characters of man and apes are less pronounced in early than in late growth stages; indeed, in embryos the similarity of certain body parts may at times verge on identity. As extreme specializations were not yet present in earlier evolutionary stages of the species, so are they lacking in early growth stages of the individual. This constitutes one of the main supports for the well-known and much contested recapitulation theory, according to which ontogeny (or individual development) repeats phylogeny (or the evolution of the species). This theory, which, at its inception, was even called a law, can not be taken literally and is to be applied with great caution. Theoretically it should be regarded as a working hypothesis and thus as a constant challenge for a possible other, and perhaps more satisfactory, explanation. However, the apparent exceptions to this theory, which have been quoted in the past in attempts to discredit it, appear to the author merely as evidence of the many other natural agencies which interfere with the exclusiveness of the principle of recapitulation by superimposing themselves on the latter.

In the search for the causes of ontogenetic changes the writer has always endeavored to look first of all for possible explanations other than those involving any phylogenetic speculations. However, if no direct causation offers itself, one is simply compelled to interpret the change as a phyletic contraction and by this is meant the inherited passing (or sometimes even permanent) re-appearance of a condition having existed in ancestral forms at some period of their growth. A great many phenomena of growth could not be understood to-day without at least this conservative version of the recapitulation theory. The tremendous amount of literature for and against this fundamental theory can not be discussed in this connection, but readers are referred at least to the critical essay by Naef (1917) and to the conclusions of Peter (1920) in regard to limiting and modifying influences on "recapitulation."

II. METHODS OF INVESTIGATION

All the detailed methods for the anthropological study of fetal growth will be described in full in another paper by the author which is to appear soon in the Contributions to Embryology (Publications of the Carnegie Institution of Washington). The justification of particulars in the technique chosen by the author, the necessary instruments, and the mathematical treatment of the data obtained will also be completely discussed in this future paper.

Since, however, the present paper deals chiefly with the ontogenetic changes in the size and proportions of the body some brief remarks have to be made in regard to the technique of measuring. To neglect this, as so many former authors have done, would render the data to be presented useless or at least unreliable for future comparative studies.

The measurements on fetuses correspond, wherever possible, in every detail to those in general use on adults. The latter have been described in full by Martin (1914).

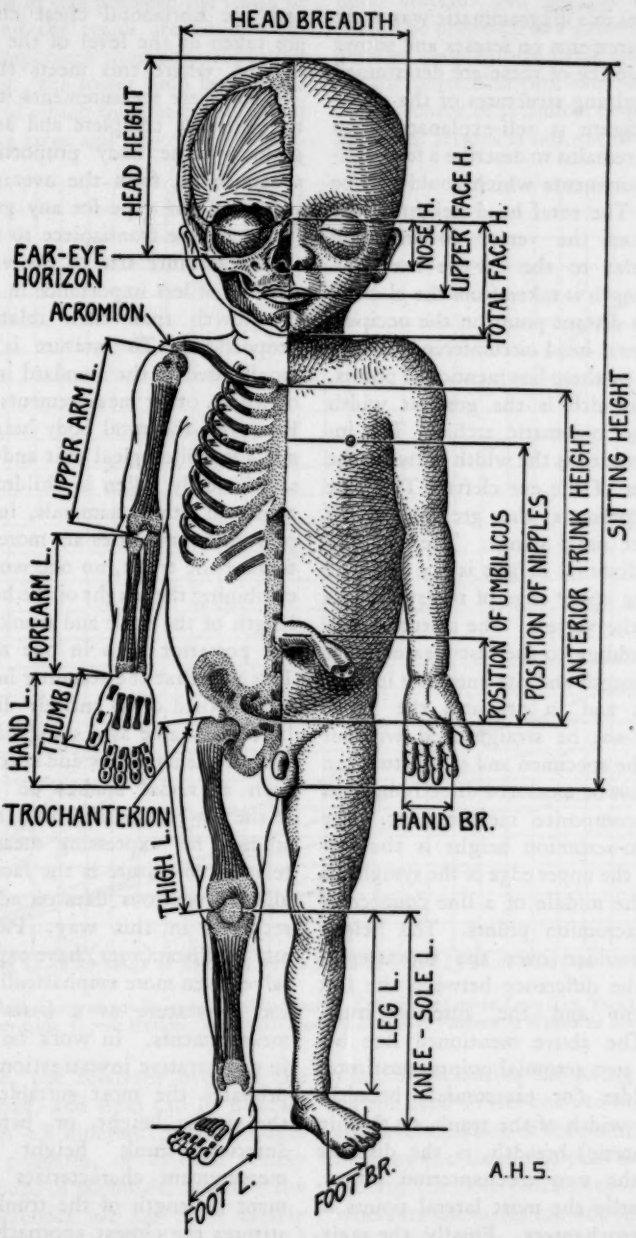

FIG. 1. DIAGRAMMATIC REPRESENTATION OF THE MEASUREMENTS TAKEN ON HUMAN FETUSES
The essential parts of the skeleton are shown on the right half of the fetus

Figure 1 gives in a diagrammatic way most of the measurements on fetuses and shows that the majority of these are determined by the underlying structures of the skeleton. The figure is self-explanatory, so that it only remains to describe a few additional measurements which could not be drawn in. The total head height is the distance from the vertex to the chin (perpendicular to the ear-eye horizon). The head length is taken from the glabella to the most distant point on the occiput. The horizontal head circumference is also determined by these last mentioned points. The face breadth is the greatest width between the zygomatic arches. The interocular breadth is the width between the inner angles of the eye clefts. The nose breadth represents the greatest width between the nasal wings. The cephalothoraco-abdominal height is the distance between the upper edge of the symphysis pubis and the vertex. The stature is obtained by adding to the last measurement the thigh length and the knee-sole length. On fetuses and in primates the lower limbs can not be straightened without injury to the specimen and the stature can therefore not be measured directly but has to be a composite measurement. The symphysion-acromion height is the distance from the upper edge of the symphysis pubis to the middle of a line connecting the two acromion points. The height of the shoulder over the suprasternal notch is the difference between the last measurement and the anterior trunk height. The above mentioned line between the two acromial points constitutes the shoulder (or biacromial) breadth. The lower width of the trunk, or the hip (bitrochanteric) breadth, is the distance between the two trochanterion points, which overlie the most lateral points of the great trochanters. Finally, the sagittal and transverse diameters of the chest and the horizontal chest circumference are taken at the level of the fourth pair of ribs, where this meets the sternum.

With these measurements it is possible to construct complete and accurate diagrams of the body proportions of any specimen or, from the average measurements, of the type for any growth stage (see e.g., the frontispiece to this paper).

The absolute size of the various body parts is of less importance in a discussion of growth than their relative size or proportions. The stature is most commonly used as the standard in percentage of which other measurements are figured. However, the total body height is really not a morphological unit and can only be satisfactorily taken in children and adult man. In other mammals, in which the posterior extremities are more or less bent toward the trunk, no one would think of combining the height of the head with the length of the neck and trunk and that of the posterior limb in one measurement. This fact that the standing height of man is composed of so entirely different units limits its value as a standard for relative measurements to few and special purposes, such as racial studies on adults. One of the few real justifications, even in racial studies, for expressing measurements in relation to stature is the fact that nearly all the previous data on adult man are recorded in this way. Pfitzner (1899) and Mollison (1911) have expressed themselves even more emphatically against the use of stature as a basis for relative measurements. In work on growth and in comparative investigations on different primates the most suitable standard is the sitting height, or, better still, the anterior trunk height. The latter measurement characterizes the development in length of the trunk. This constitutes the closest approach to a perfect standard for the main body proportions.

The relations in size between the limbs or the head and the trunk are unquestionably more important than the proportion between, e.g., the lower limb length and the stature, of which the first measurement itself forms a large and very variable part. Furthermore, the relations between the limbs, or head, and stem can be directly compared in all different growth stages and in all primates, or in even widely different groups of mammals, whereby the typical differences are far more clearly brought out than in proportions based upon stature. No general rule can or should be proposed as a guide for the many detailed proportions; these are determined by the particular problems to be solved.

The source of technical error in measuring small fetuses is not necessarily greater than in measuring the living adult, since on the dead fetuses one can readily control the determination of the points of measurement by the aid of fine pins or even by dissecting the soft parts over the skeleton, wherever the latter can not be palpated on the surface with absolute certainty. The

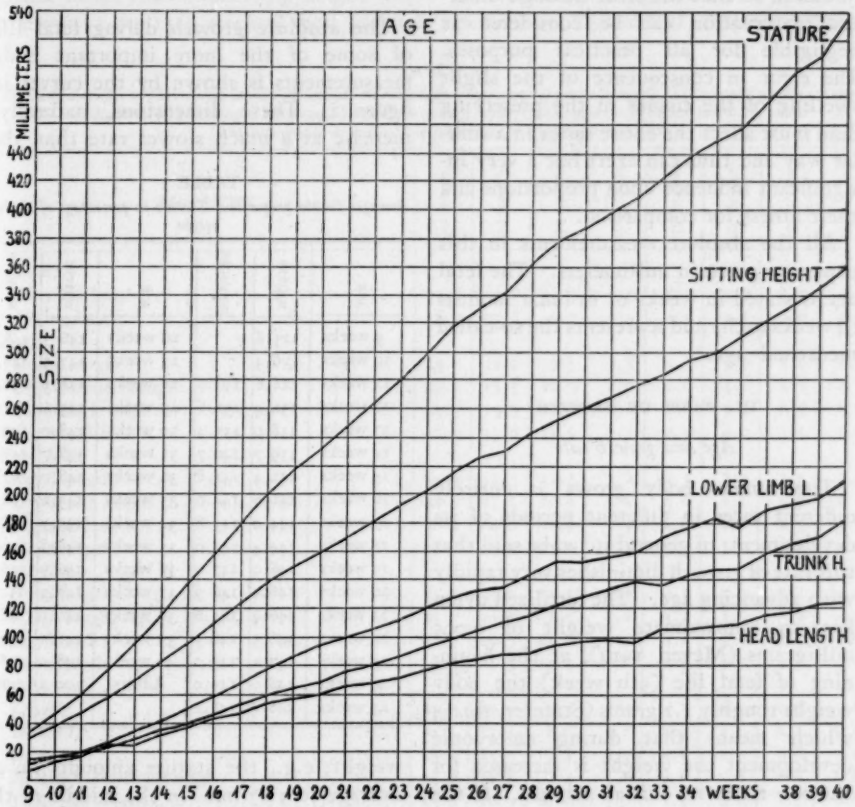

FIG. 2. CURVES OF GROWTH FOR STATURE, SITTING HEIGHT, LENGTH OF LOWER LIMB (GR. TROCHANTER TO SOLE) ANTERIOR TRUNK HEIGHT, AND HEAD LENGTH OF WHITE FETUSES (9 WEEKS TO BIRTH)

preservation of fetuses introduces a possibility of artificial changes, as was shown by the author (1919) on some special experiments. However, more than 96 percent of the material, used in this study, was preserved uniformly in 10 percent formalin, so that the error through different preservation can be considered as negligible for all practical purposes. The error in consequence of the slight swelling of the tissues in the preserving fluid must affect the entire series in a similar way and thus can exert but a very insignificant influence upon proportions and their fitness for comparison.

All the absolute measurements in this paper are given in millimeters. The fetal age is stated in weeks or in lunar months (4 weeks each) and represents the so-called menstrual age.

III. RATES OF GROWTH

Age and growth rate

The human body grows at entirely different rates in different periods of its development; in general it can be said that this rate of growth diminishes very rapidly with advancing age. The fertilized ovum has an approximate weight of 0.005 milligrams (Meyer, 1914), at the beginning of fetal life (9th week) the body weighs roughly 1.1 grams (Streeter, 1920), which means that during embryonic development the weight is increased for 220,000 times its initial amount. If the average weight of the white newborn is placed at approximately 3200 grams, the increase during fetal growth equals 2,900 times the weight at 9 weeks. Finally, during life after birth the weight of the newborn is increased only about 20 times. In relation to time these growth rates are even more strikingly different, since embryonic life lasts roughly 8 weeks, fetal life 32 weeks, and postnatal growth about 1000 weeks. In the first period the weight increases on an average per week 27,500 times, in the second or fetal period 90 times, and in the last growth period only 0.02 times.

Growth rates in different parts of the body

The absolute growth during fetal life of some of the more important body measurements is shown by the curves in figure 2. These dimensions, naturally, increase at a much slower rate than the weight; e.g., the stature amounts on an average to 32.7 mm. in the middle of the 9th week and to 532.1 mm. at birth, an increase of only 16.3 times the initial value. The different curves do not proceed in a constant relation to each other, but manifest a certain independence. This is best shown on the example of the percentage relation between stature and sitting height, which is given in table 1. At 9 weeks of fetal life the standing height exceeds the sitting height by only 15.8

TABLE 1

Averages for the proportion: Stature in percentage of sitting height

AGE	WHITES	NEGROES	AGE	WHITES	NEGROES
9 weeks	115.8		26 weeks	146.7	148.2
10 weeks	126.4		27 weeks	147.3	148.3
11 weeks	128.6	130.0	28 weeks	148.3	151.6
12 weeks	132.4	132.6	29 weeks	149.2	151.1
13 weeks	138.0	135.4	30 weeks	148.0	149.0
14 weeks	139.7	140.7	31 weeks	148.7	150.2
15 weeks	142.4	141.8	32 weeks	148.0	147.3
16 weeks	142.6	144.0	33 weeks	149.2	148.9
17 weeks	144.0	143.8	34 weeks	147.7	148.8
18 weeks	144.4	143.0	35 weeks	148.8	150.4
19 weeks	146.0	147.0	36 weeks	146.9	146.7
20 weeks	146.4	146.9	37 weeks	147.5	151.4
21 weeks	146.4	145.6	38 weeks	148.0	148.9
22 weeks	146.5	148.5	39 weeks	146.2	149.8
23 weeks	147.2	149.0	40 weeks	148.0	148.8
24 weeks	148.0	149.0	Adults	200.2	201.7
25 weeks	148.4	148.2			

percent of the latter, at the end of the 6th month the former measurement is nearly one and a half times as long as the latter measurement, and in adults the stature equals about twice the sitting height. In other words, the total body height grows much faster than the sitting height from the 9th to the 15th week of fetal life and negroes have the slightly higher values, is already clearly indicated in fetuses, since in 22 week groups the negro fetuses have higher averages than the white fetuses, whereas in only 9 groups is this relation reversed. The higher this index the relatively longer are the lower extremities. This racial difference means,

TABLE 2

Monthly averages of the relative weekly increments in some body dimensions of white fetuses. The relative weekly increment is obtained by expressing the difference between the averages of a given measurement in two successive weeks (absolute weekly increment) in percentage of the smaller average

MEASUREMENT	3RD MONTH	4TH MONTH	5TH MONTH	6TH MONTH	7TH MONTH	8TH MONTH	9TH MONTH	10TH MONTH
General:								
Standing height	32.6	19.8	10.5	6.5	5.1	3.0	2.7	4.0
Sitting height	26.7	17.6	9.7	6.4	4.9	3.1	3.0	3.8
Trunk:								
Trunk height	29.2	18.0	9.5	8.2	5.7	5.0	1.6	5.3
Chest circumference	23.2	19.3	10.7	6.0	2.6	4.2	2.3	4.7
Shoulder breadth	24.3	19.3	11.1	6.2	4.8	3.4	2.5	6.2
Hip breadth	31.0	23.6	11.5	7.5	4.3	4.0	3.1	5.6
Upper limb:								
Total length	39.3	23.3	11.1	5.8	4.5	2.5	3.1	4.4
Upper arm length	44.5	23.2	10.3	5.2	4.0	2.1	2.9	4.4
Forearm length	46.4	24.0	10.9	5.3	4.0	2.6	2.5	4.9
Hand length	26.0	22.3	12.6	7.3	5.9	3.1	4.2	4.0
Lower limb:								
Total length	45.5	24.2	12.3	6.9	4.1	2.9	3.1	4.0
Thigh length	45.7	23.0	11.5	6.8	3.7	3.5	2.7	4.1
Leg length	48.7	26.5	12.6	6.7	4.4	2.4	3.3	3.6
Foot length	29.5	21.9	13.4	8.2	5.9	3.0	3.7	4.0
Head:								
Length	22.0	17.0	9.9	5.9	4.2	2.4	2.7	3.1
Breadth	22.2	17.4	8.7	5.1	3.5	3.6	2.3	2.3
Height	24.0	15.3	9.4	4.5	4.6	1.7	2.8	3.1
Horizontal circumference	24.9	16.6	9.4	5.8	3.6	2.8	2.8	2.6
Total face height	25.0	16.9	11.0	5.7	3.3	4.6	1.7	3.3
Face breadth	23.5	19.5	9.5	4.9	3.2	3.3	2.6	3.0

again during postnatal development. From the 15th to the 20th week the difference between the growth rates of these measurements is but little, and between the 6th month and birth the two grow about equally fast. Incidentally, table 1 shows also that the racial difference in this proportion, according to which adult therefore, that negroes have in general proportionately longer legs than whites (see also Bean, 1922).

Fluctuations in growth rate

It has been shown above that in general the rate of growth diminishes very markedly with advance in age and that different

parts of the body grow at times with different intensity. Both these general rules, in their particular application to fetal growth, are very evident in the figures listed in table 2. The relative increments of all the various measurements are far higher in the first than in the last part of fetal life. However, the decrease in these increments is not quite continuous, since it changes in most measurements to a slight increase during the last few months before birth. Thus, the actually lowest rate of growth occurs in the stature, sitting height, and trunk measurements during the 9th month, in the majority of the limb measurements during the 8th month, and in most of the head measurements during the 8th or 9th month. This indicates a certain periodicity for fetal growth, similar to the well known fluctuations in the growth rates after birth which are not restricted to man, but are found in other animals as well (e.g. Gartner, 1922). Of the many papers dealing with the periodicity of postnatal growth only the first and last can here be mentioned, namely those by Zeising (1854) and by Bean (1923, 1924).

Alternations in growth rate

Besides these fluctuations there occur clear alternations in the growth rates of different parts of the body. For instance, as shown by table 2, the relative increments for the trunk height are greater than those for the chest circumference and shoulder breadth in the 3rd month of fetal life. In the 4th and 5th months this relation is reversed, only to change back again in the 6th, 7th, and 8th months, and to change a third time in the 9th and 10th months to a preponderance in rate of growth in width over that in height. Not only growth in height and width alternate in intensity—producing successive periods of "streching" and of "filling"—but also growth in such adjoining parts of the body as the different segments of a limb. For instance, the most distal parts of the extremities, the hand and foot, grow more slowly than the more proximal parts during the 3rd and

FIG. 3. SCHEMATIC REPRESENTATION OF THE RELATION BETWEEN FOOT LENGTH AND LEG LENGTH (LENGTH OF TIBIA) AT DIFFERENT GROWTH STAGES

All the tibiae have been drawn to the same length (= 100). The proportions of these drawings are based upon the averages of measurements on large series of whites.

the 4th months, whereas from the 5th to 9th month the relative increments of the upper arm and forearm surpass those of the hand and the increments of thigh and leg are larger than those of the foot. In a similar way alternate the growth rates in the trunk height and in the total limb lengths, the latter increasing faster than the former during the 3rd, 4th, and 5th months, but more slowly in the 6th, 7th, and 8th months and again in the 10th month, while in the 9th month it is once more the trunk which grows at the slower rate (see table 2). Such alternations in growth rate also take place during postnatal life, only there they are spread over much longer periods, which are reckoned in years rather than in months (e.g. Godin, 1903 & 1910 a).

These changes in the relation between the intensities of growth in different body parts determine directly the changes in the proportions during development. An illustration of this is given by figure 3 which shows the striking fluctuations in the proportion between the lengths of foot and leg. At 9 weeks of fetal life the human foot is very much longer than the leg, at 15 weeks the leg has become the longer of the two on account of the much slower growth rate in the foot than in the leg, but at birth both are nearly equal in length. During growth after birth the leg again increases faster than the foot, reducing the length of the latter to 69 percent of that of the former.

Growth rate and species differences

Different proportions in adult primates with divergent specializations can often be traced to differences in growth rates, as shown by the example in figure 4. In early fetuses the three segments of the upper extremity have practically the same proportionate lengths in man and gibbon; the middle segment at this time is the shortest in both. In older fetuses the forearm has surpassed the hand in length in man and ape. Not until birth appears the peculiarity of the gibbon, i.e., a forearm exceeding in length the upper arm, and even then this is just barely indicated. The great lengthening in the upper extremity of the gibbon, which is unequaled in its proportionate amount by any other primate, takes place most of all in the forearm, but the excess of the latter over the upper arm becomes most pronounced only at the completion of growth. Thus, it can be said that it is primarily a difference in relative rate of growth which brings about the difference in the arm proportions between adult man and gibbon.

Law of developmental direction

This chapter on the rates of growth can not be closed without some brief remarks bearing on the so-called law of anteroposterior development (Child, 1915), or of cephalocaudal differential growth (Kingsbury, 1924, 1926) which is also called the law of developmental direction (Jackson, 1914). According to this law, the early differentiation of the embryo, as well as its later development, proceeds in general in all vertebrates in the head-to-tail direction, so that the more caudal parts of the body are for a considerable period a step behind the more cephalic parts in their development. This, for instance, is evident from the fact that the arm bud antecedes the leg bud in its appearance. This acceleration in the development of the upper extremity, or retardation in that of the lower extremity, is not confined to embryonic growth but clearly persists even to advanced stages of fetal life. Illustrations of this are furnished by the following notes from the author's observations on human fetuses: The separation of the fingers occurs earlier than that of the toes.

The touch pads on the hand can be either dimly recognized or have disappeared altogether in fetuses (of about 12 weeks) in which the plantar touch pads are still well defined. In many fetuses of about the 22nd week sparse and very short bear already hairs of considerable length. The papillary ridges develop slightly sooner on the palm and fingers than on the sole and toes. Fetuses of the 6th month have ossified zones in all the middle phalanges of the fingers, but in the

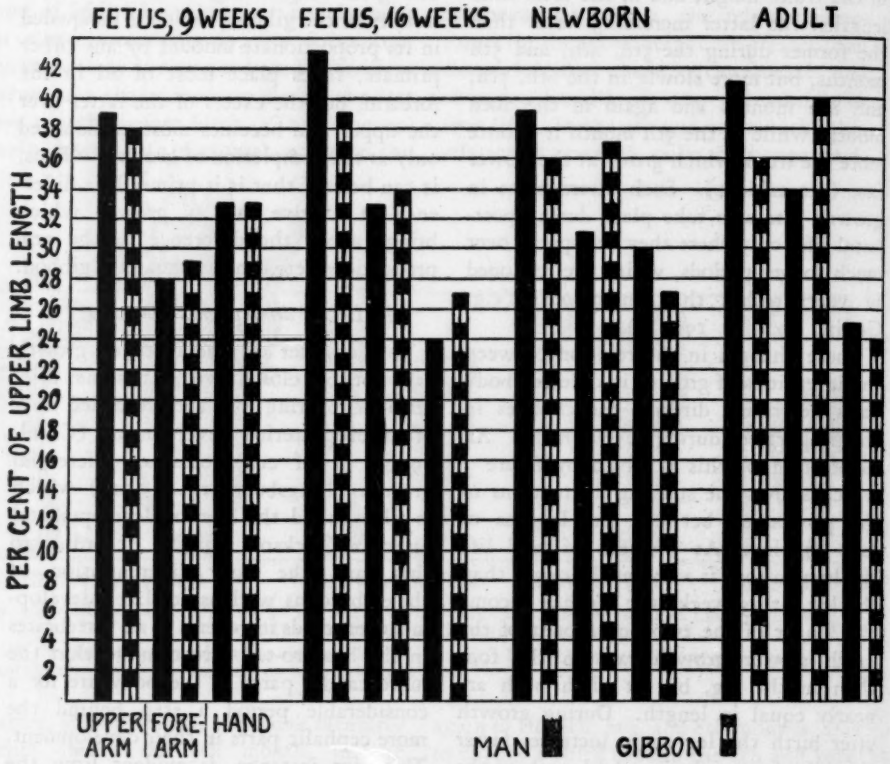

FIG. 4. DIAGRAM OF THE GROWTH CHANGES IN THE PROPORTIONS OF THE UPPER LIMB OF MAN AND OF GIBBON

The perpendicular rods represent the lengths of the upper arm, forearm, and hand in percentage of the total upper limb length. The values for man are averages from large series of whites. The values for gibbon are those of a *Hylobates concolor* (sitting height 21.5 mm.) corresponding in development to a human fetus of 9 weeks, and for the older growth stages of *Hylobates pileatus*, i.e., of a fetus (83 mm. sitting height) corresponding to a 16 weeks old human fetus, of a newborn (198 mm. sitting height), and of the averages of six adults.

lanugo can be made out of the upper arm (particularly near the elbow), while no hair at all can be detected on the lower limbs of the same specimens. In slightly older fetuses, in which the lanugo on the thighs has just become visible, the arms

toes these phalanges have either no trace of ossification as yet or only for the second and third toes.

Since the more cephalic parts of the body have a higher initial rate of growth than the more caudal parts, it can be con-

cluded that the latter must subsequently grow at a higher rate in order ultimately to catch up, so to speak, with the former. This could be shown on many examples, but it suffices to mention a few: The lower width of the trunk (hip breadth) in white fetuses forms at 9 weeks only 58 percent of the upper width (shoulder breadth), however, from the 3rd to 6th month the former grows very much faster than the latter (see tables 2 and 4), raising the proportion between the two measurements to 83 at the 24th week. In young fetuses the cervical region of the spine is more developed than the lumbar region, the former constituting 26 percent of the praesacral spine length, the latter only 25 percent. In the course of growth the relative length of the lumbar region soon surpasses that of the cervical region, which in adults has decreased to 22 percent, while the lumbar region has become lengthened to 32 percent.

TABLE 3

Growth changes in the proportion: Chest circumference in percentage of anterior trunk height. The indices for man are approximate means, those for other primates are based upon single specimens. The development (but not the actual age) of the different monkey fetuses in a given perpendicular column corresponds approximately to that of human fetuses of the stated age in the particular column

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th–5th	6th–8th	9th–10th	Infant	Juvenile	Adult
Man (Whites)	223.0	216.0	197.0	184.0	179.0	173.0	170.0
Orang-utan		213.1	208.6	208.2	197.3	209.2	209.5
Gibbon	198.3	199.4	180.6	173.4	168.6	167.9	148.0
Baboon		155.2	144.7	143.0	143.0	142.6	140.2
Macaque			156.6	141.9	129.2	110.3	104.5
Proboscis monkey		140.5	136.6	123.2			97.8
Colobus monkey		144.0	137.5	124.7		98.7	90.7
Capuchin monkey		144.6	150.4	135.3	131.7	127.4	129.5
Spider monkey			190.1	170.2	165.0	140.4	122.4
Howler monkey	175.8	176.4	162.5	152.2	142.8	141.2	149.2

IV. TRUNK

Chest circumference

The trunk becomes in general more and more slender with advancing growth. This is clearly shown by the age changes in the relation between chest circumference and trunk height, listed in table 3. In human fetuses of the 9th week this percentage proportion averages 238, in adult man only 170. In other primates the values for young fetuses are also higher than those for adults. In the orang-utan and in the howler monkey the figures indicate a tendency for a late secondary increase in this proportion, however, the individual variability in the relative chest girth is so marked in all primates that data on many more specimens are required to render this conclusion final. Should it prove to be correct, it would correspond closely to the slight secondary increase in the relative chest circumference of man between the ages of puberty and about 40 to 50 years. It is interesting to note that the amount of ontogenetic change in the relative stoutness of the trunk is very different in different primates. For instance, in the spider monkey the index drops between the fetal age of 6 to 8 months and adult life for 68 units, while in man, in the same interval, for only 27 units, and in

the baboon for only 5 units. Of special significance is the fact that the range (difference between minimum and maximum, table 3) of this index among primates of corresponding development becomes steadily larger with advance in growth. Thus, the range among fetuses of 6 to 8 months amounts to 72 units, or 43 percent of the average index in that column; in fetuses, 9 to 10 months old, it is 85 units (= 55 percent of average); in juvenile primates the range amounts to 110 units (= 75 percent), and in adults to 119 units (= 87 percent). It can be stated, therefore, that even in fairly old primate fetuses the divergent specializations in the trunk shape have as yet advanced only about one half as much (relative difference between extremes 43 percent) as in adult primates (extremes 87 percent apart).

TABLE 4

Averages of the proportion: Hip breadth in percentage of shoulder breadth in white and negro fetuses and adults

AGE	WHITES	NEGROES	AGE	WHITES	NEGROES
9 weeks	58.2		26 weeks	80.5	81.5
10 weeks	62.4		27 weeks	78.5	75.4
11 weeks	63.4	64.8	28 weeks	81.7	80.8
12 weeks	68.0	64.6	29 weeks	78.3	75.3
13 weeks	69.8	66.4	30 weeks	79.2	75.8
14 weeks	74.3	69.2	31 weeks	80.5	82.7
15 weeks	74.9	76.5	32 weeks	83.9	79.1
16 weeks	78.2	76.0	33 weeks	84.8	79.3
17 weeks	79.2	77.5	34 weeks	86.6	82.8
18 weeks	80.5	80.3	35 weeks	87.1	78.9
19 weeks	80.2	78.9	36 weeks	85.8	79.3
20 weeks	79.4	77.1	37 weeks	83.3	84.4
21 weeks	82.1	81.6	38 weeks	88.2	77.7
22 weeks	82.4	78.3	39 weeks	82.0	82.9
23 weeks	81.8	83.3	40 weeks	84.0	80.5
24 weeks	83.3	82.4	Adults	90.9	86.7
25 weeks	84.0	82.0			

Hip breadth

With advance in growth the human trunk becomes relatively broader at its lower end, i.e., the hip breadth increases faster than the trunk height, a conclusion which is also reached from a comparison between the increments in these two measurements, as listed in table 2. In white fetuses of the 9th week this relative hip breadth (hip breadth in percentage of trunk height) averages 42.3, at the end of the 4th month it has increased to 53.3, from then to birth it remains in general stationary, only to increase a second time during growth after birth, reaching an average of 61.5 in adult white men. This important and very marked age change escaped entirely the attention of Retzius (1904), who expressed the pelvic width in relation to body length, concluding that no changes in this proportion occur during fetal life. Weissenberg (1911) also formed an index of the hip breadth and stature in a small series of fetuses and finds it to decrease with advancing age. These two examples show again how misleading it can be to use stature as a standard in the study of growth. The conclusions of these authors are explained by the fact that any proportional increase in the width between the hips is, especially in early development, neutralized or even surpassed by the rapid increase in length of the lower extremity which forms part of the stature. Friedenthal (1914), who figured the relative hip breadth in the same way as the writer, finds it to increase during the first part of fetal growth, which is in strict agreement with the result of the author.

A few examples will suffice to show that, as in the last proportion so in this one, not only occur the age changes in various primates in a very similar way but the differences in this index between man and apes or monkeys are again much smaller in fetuses than in adults. In a gibbon fetus (*Hylobates concolor*, 56 mm. sitting height) the relative hip breadth

amounted to 39.0, in an adult of the same species to 48.8, that is a difference from the human conditions at corresponding stages of growth of 5.3 index units in case of the fetus and of 12.7 in the adult. In a howler monkey fetus (*Alouatta palliata*, 48 mm. sitting height) this proportion is 30.6, and in a full-grown specimen 43.2; the former value lies 11.1 units below that of a human fetus of corresponding development, the latter 18.3 units below that of adult man.

The relation between the upper and the lower width of the trunk is of considerable anthropological interest and this not only on account of the marked growth changes in this porportion but also for its clear racial difference. According to table 4 the two breadth diameters of the trunk approach one another more and more with advancing age. Similar ontogenetic changes occur in other primates besides man (see figure 5), e.g., the index amounts to 66.8 in a gibbon fetus (56 mm. sitting height) and to 71.8 in an adult of the same species (*Hylobates concolor*); in a macaque (*Pithecus rhesus*) it is 77.3 in a fetus (167 mm. sitting height) and 119.6 in an adult; in a howler monkey (*Alouatta palliata*) it amounts to 55.4 in a fetus (48 mm. sitting height) and to 109.2 in an adult. This index among primates seems to be correlated to a certain extent with their particular modes of progression. In those forms which are entirely quadruped, walking on all four limbs either on the ground, like the baboons, or on top of branches, like the howler monkey, the shoulder breadth is comparatively little developed, being less than the pelvic breadth in the adult. On the other hand, in primates which chiefly hang by their arms, like the gibbon, the orang, and the spider monkey, the shoulder width is relatively broad and thus retains its fetal relation to the pelvic width more closely than in the first group. The percentage relation between hip breadth and shoulder breadth of adults amounts in the first group of primates always to more than 100, namely to 119.4 in a baboon (*Papio hamadryas*), 119.6 in a macaque (*Pithecus rhesus*), 109.2 in a howler monkey (*Alouatta palliata*), and in marmosets and lemurs, which also do not habitually hang from branches, to 113.0 in a *Saimiri sciureus*, to 104.6 in a *Seniocebus bicolor*, to 101.0 in a *Leontocebus geoffroyi*, to 117.6 in a *Callithrix pennicillata*, and to 126.6 in a *Lemur variegatus*. In the second group—the forms specialized for swinging by their arms—the index is always considerably less than 100, namely 78.7 in an orang-utan, 71.8 in a gibbon (*Hylobates concolor*), 70.9 in another gibbon (*Hylobates lar*), and 92.4 in a spider monkey (*Ateles geoffroyi*).

Man, with a use of his limbs different from that of any other primate, stands in regard to this index between the extremes of the two groups discussed (gibbon 71, man 87–91, baboon 119). Again it should be mentioned that fetuses are less different in this respect than adults. For instance, at stages of development, corresponding to the end of the 5th fetal month in man, the index is in a gibbon 70.0, in man about 80, and in a baboon 90.2; i.e., a difference between the extremes of 20 units in the middle of prenatal life as compared with 48 units at completion of growth.

The human racial difference in this proportion is quite marked in the adults (see also Martin, 1914), negroes having relatively narrower hips than whites. This difference is already clearly indicated in fetal life, since the higher averages are found in whites in 23 out of the 30 week groups, for which fetuses of both races could be examined. The figures for adults in table 4 are averages for series of males. In women the index is in most, if not all, races higher than in

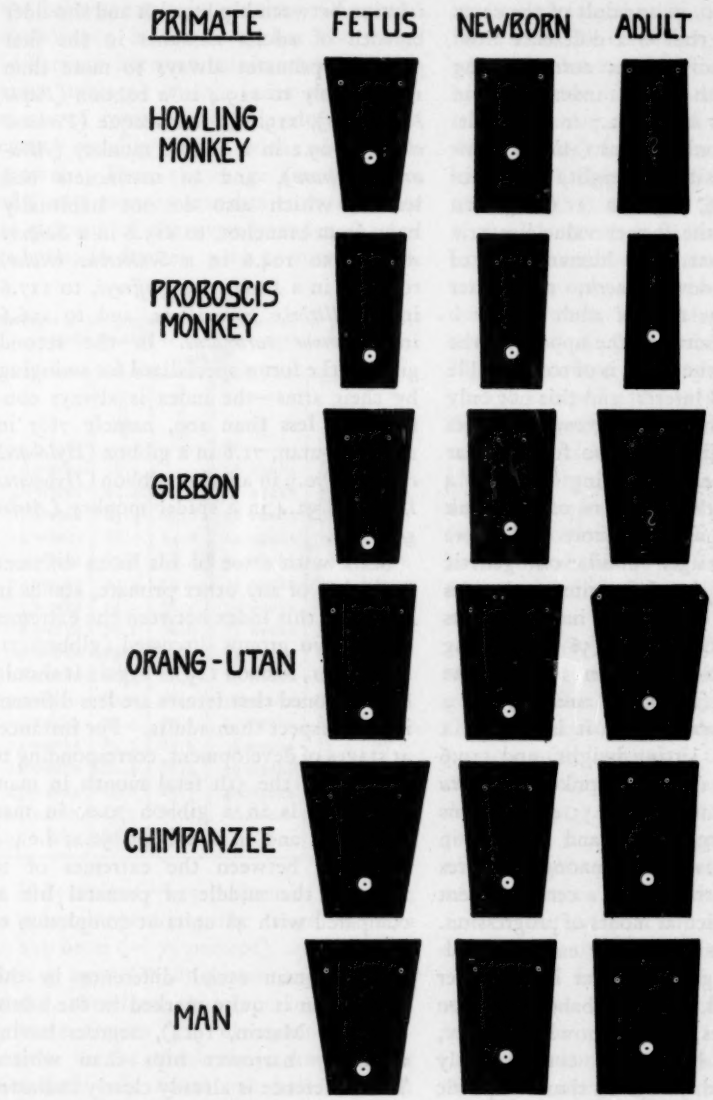

FIG. 5. DIAGRAMMATIC REPRESENTATION OF THE GROWTH CHANGES IN THE TRUNK OF VARIOUS PRIMATES

The diagrams are constructed from the anterior trunk height (drawn to equal the same size in all figures), the shoulder breadth, and the hip breadth. The exact position of the nipples of the umbilicus is shown in the figures. The fetuses of man, gibbon, and howler monkey are approximately of the same stage of development (3rd month in man), those of the other primates are somewhat older (roughly corresponding to the 5th month in man).

men, a difference which, like nearly all secondary sex differences, does not become very marked until rather late in postnatal growth.

Nipples

The diagrams in figure 5 show that during growth the nipples shift their relative position on the anterior trunk wall in a cranial direction in all the primates, except man. In the latter the nipples move in a caudal direction on the trunk during the 3rd, 4th, and 5th fetal months, from then to birth there prevails a tendency toward a relatively higher position, to change back to a secondary and marked downward migration of the nipples during postnatal growth. In relation to the ribs the human nipples change ontogenetically in the same sense, since in young fetuses they overlie the second intercostal space, and in adults they have reached the fourth or fifth ribs. The percentage relation between the distance from the level of the nipples to the upper edge of the symphysis pubis and the anterior trunk height expresses accurately the relative position of the nipples. This index amounts to about 71 in adult negroes and to about 74 in adult whites. In all other adult primates the values are higher (see also Mollison, 1911). In individual cases there may be but little difference, particularly among the macaques and baboons (e.g., one ♀ ad. *Pithecus speciosus* 74.5, one ♂ ad. *Papio hamadryas* 76.8, and one ♀ ad. *Pithecus nemestrinus* 78.7), but the great majority of monkeys and apes have very much higher indices than man, indeed, in some the nipples lie close to the suprasternal notch or right in the axillae. Such extremly high nipples are found particularly in orang-utan (ad. ♂ 93.4), in the howler monkeys (ad. ♂ *Alouatta palliata* 97.8, ad. ♀ *A. seniculus* 99.6), in spider monkeys (ad. ♂ *Ateles geoffroyi* 92.6, ad. ♂ *A. neglectus* 92.7), and among marmosets (ad. ♀ *Callithrix penicillata* 92.9). From these notes it can be concluded that, whereas man has the lowest placed nipples of all adult primates, this human distinction does not come about until late in growth, since in fetuses the nipples of monkeys are relatively lower, and those of man relatively higher, situated than in the respective adults. Furthermore, it seems justifiable to assume that the extreme positions of the nipples among primates are most likely late phylogenetic specializations, as they are late ontogenetic acquisitions. An orang-utan fetus (145 mm. sitting height) has an index for the relative position of the nipples of 84.9; human fetuses of the same stage of development (5th month) have an average index of 76.6 (negroes) but vary individually to a maximum of 85.9. During later growth the changes in this index diverge rapidly, causing it to rise to 93.4 in adult orang and to drop to 71 in adult negroes.

Umbilicus

In a great many adult monkeys there is absolutely no trace of an umbilical scar left and even in some juvenile primates can the umbilicus not be found. This complete absence of any umbilical scar has also been noted on other mammals (Levadoux, 1907). In all primates the umbulicus shifts in the course of growth to a relatively higher position on the trunk, as shown by the examples in figure 5, indicating a greater rate of growth in the lower than in the upper part of the trunk. This is further demonstrated by the first column of figures in table 5. These figures express the distance from the center of the umbilical cord or scar to the upper edge of the symphysis pubis in percentage of the

anterior trunk height. The relative position of the umbilicus is closely correlated to the relative length of the lumbar region of the spine, i.e., the shorter the latter the relatively lower lies the umbilicus and *vice versa*. This is true in regard to different primates as well as to the changes during growth (see table 5), and Soularue (1899) pointed out that even the slightly higher position of the

TABLE 5

*Correlation between the relative position of the umbilicus and the relative length of the lumbar portion of the spine (in percentage of the praesacral spine length) during growth and in different primates. Figures marked * calculated from data given by Mollison (1911), those marked † after Keith (1903)*

PRIMATE	AGE	RELATIVE POSITION OF UMBILICUS	RELATIVE LENGTH OF LUMBAR REGION
Orang-utan	Fetus	17.3	22
	Infant	18.0	23
	Adult	21.2*	24†
Chimpanzee	Infant	22.3	24
	Adult	25.9*	27†
Gorilla	Adult	27.0*	29†
Man	Fetus	18.5	25
	Infant	26.1	27†
	Adult	28.2*	32†
Gibbon	Fetus	21.4	23
	Infant	23.3	28
	Adult	30.0*	32†
Macaque	Adult	35.0*	42†

umbilicus in women than in men is connected with a relatively longer lumbar spine in the former than in the latter. Among adult primates the anthropoid apes have the lowest placed umbilicus, man comes next in this respect, then the gibbons, while in the large majority of the monkeys and, particularly, the lemurs the umbilicus is situated much higher on the trunk (Mollison, 1911). The developmental changes in this bodily character are most likely due to the above mentioned law of cephalocaudal growth, and have no particular phylogenetic significance besides the fact that their remarkable uniformity in all primates (of which only a few examples can be listed in table 5) speaks for their close relationship.

Chest shape

The transverse and the sagittal diameter of the chest are of special interest in their relation to one another. The latter is expressed in the chest index, which indicates the general shape of a horizontal section through the thoracic region of the trunk at the level of the sternal attachment of the fourth ribs. With advance in growth the human chest becomes relatively broader, i.e., the chest index increases on account of a greater rate of growth in the transverse than in the sagittal diameter. The deep and narrow chest of the human embryo has been described by Müller (1906) and by Rodes (1906). According to the latter author human embryos and young fetuses have chest indices of 55.1, 66.6, 77.9, and 105.2 respectively at 4, 5½, 7, and 10 weeks of age. These figures were obtained from measurements taken at the level of the lower end of the sternum, but Rodes states that the proportion between these diameters differs but little from that between measurements higher up on the thorax. The writer found the chest index to change during growth from an average of 104.6 at 9 weeks of fetal life to 118.4 at 12 weeks, to remain in general the same from then to birth, and to increase again during postnatal life to at least 130.5 in white men of about 25 years.

Immediately after birth, i.e., with the beginning of breathing, the chest index undergoes according to Scammon and Rucker (1921) a sudden drop, which is

apparently not recovered until some weeks after birth. The indices given by these authors are, when figured in the way used in this paper, 116.2 at birth, 94.3 15 minutes after birth, 98.0 12 hours after birth, and 99.5 at the 10th day.

As shown by table 6, the growth changes in the chest index are principally the same as in man in the orang and gibbon (and probably also in chimpanzee and gorilla, for which, however, no sufficient data are available as yet). On the other hand, in the great majority of the lower primates the chest shape changes with age in just the opposite way, i.e., it becomes steadily narrower. Thus it is found that as widely different indices of adult primates, as that of man (average 130) and of the howler monkey (individually as low as 78), have ontogenetically the same starting point, namely 110 in human fetuses of the 3rd month and as much as 109 in howler fetuses of similar development.

Some authors (e.g., Wiedersheim, 1908) familiar only with the growth changes in the human chest, have advanced the theory that the narrow and deep chest of human embryo represents a recapitulation of an ancestral condition, particularly of a quadruped form in which the thorax was suspended beneath the spine. The human chest shape unquestionably resembles that of adult quadrupeds much more in fetal than in adult life, as is clearly shown by the examples in figure 6. However, in very young dog fetuses the chest diameters are still the same in the transverse as in the sagittal direction, so that, in order to be consistent, one would have to make the absurd assumption that the ancestors of the dog had an upright posture. The chest shape in early embryonic life can not be regarded as the ontogenetic re-appearance of some phylogenetic condition, but is directly determined by causes of a purely topographic nature, especially by the growth of heart, lungs, and liver. After birth gravity is the most potent factor influencing the thorax shape. In quadrupeds the weight of the organs exerts a constant pressure on the sternum, thereby tending to increase the depth of the chest. In man the weight of the thoracic organs acts in a different direction, i.e., on the diaphragm. Finally, in the sloth, which habitually assumes an upright position or hangs even suspended by all four limbs, gravity affects the chest in just the opposite di-

TABLE 6

Growth changes in the proportion: Transverse chest diamster in percentage of sagittal chest diameter. The indices for man are approximate means, those for other primates are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th–5th	6th–8th	9th–10th	Infant	Juvenile	Adult
Man (Whites)	110.0	117.0	117.0	118.5			130.5
Orang-utan		111.5	110.0–112.0	115.2	115.5–123.4	132.2–135.4	155.6
Gibbon	98.4–112.6	113.3–117.3	106.0–114.2	115.3–123.0	117.8–115.7	115.5–117.8	129.4
Baboon		95.9	94.6–97.5	87.6–92.7	86.9–89.4	80.8–85.6	84.4
Macaque		101.3	93.0–96.0	90.7	89.2–90.0	89.2–92.1	81.8–90.3
Colobus monkey		104.3	96.8–106.6	103.2		89.8	90.4
Capuchin monkey		96.4	95.9		92.9	90.0–92.9	88.2– 93.3
Howler monkey	100.0–109.3	106.3–108.2	102.5–102.9	97.0–106.4	95.4–102.3	92.1–100.0	78.1–100.0

rection as in quadrupeds, producing a chest index of 160, in contrast to one of about 72 in the adult dog. Table 7 demonstrates that the chest index of the sloth increases ontogenetically, while that of the dog, as mentioned above, according to anthropological usage) of 88.9, in another dog from the same litter this index had decreased in adult life to 74.5. In a third dog of this litter the index remained practically constant, amounting to 86.6 in the full-grown

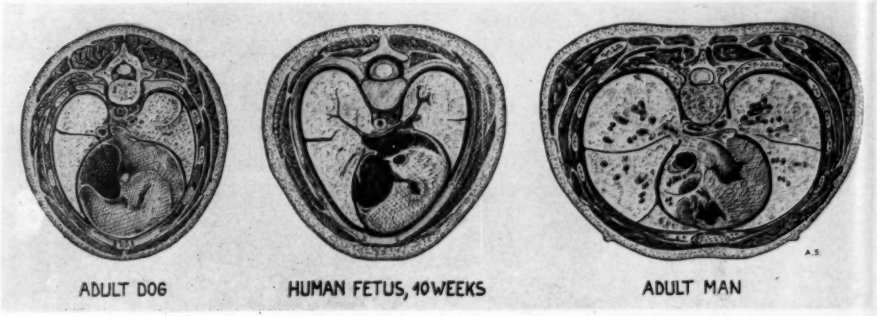

FIG. 6. CROSS SECTIONS OF THE CHEST IN AN ADULT QUADRUPED, A HUMAN FETUS, AND ADULT MAN, SHOWING THE PROFORTIONS BETWEEN THE TRANSVERSE AND SAGITTAL DIAMETERS

TABLE 7

Growth changes in the chest index of the sloth (Bradypus griseus). The "length" of the specimens represents the length of the spine without the tail

AGE	LENGTH	CHEST INDEX
Fetus	49	102.9
Fetus	77	104.0
Fetus	90	102.8
Fetus	101	103.8
Fetus	103	104.4
Fetus	118	106.1
Fetus	130	107.1
Fetus	134	110.3
Fetus	135	110.0
Fetus	150	112.0
Fetus	171	110.8
Newborn	172	112.8
Adult ♀	465	155.4
Adult ♂	480	159.5

decreases. By far the greatest increase occurs in the sloth during growth after birth, when gravity comes into play.

The influence of gravity on the chest shape of the dog was shown experimentally by Jackson (1907). A newborn puppy had a thoracic index (when figured

animal, and this on account of the fact that the dog had been forced to assume an upright position for 12 hours daily during one year. The author of this experiment had expected an even more marked effect of gravity on the last mentioned animal, but this seems hardly justifiable.

Height of shoulder

This discussion of the most important growth changes in the trunk would not be complete without some mention of the relative height of the shoulders. The latter is determined by the perpendicular distance between the level of the acromial point on the shoulder (see fig. 1) and that of the suprasternal notch. The greater this distance the steeper is the direction of the clavicles; on the other hand, the clavicles are horizontally posed in case the shoulders occupy one level with the suprasternal notch. From the figures in table 8 it is evident that the shoulders stand relatively higher in fetal than in

adult life of man. The most marked descent of the shoulder takes place in the white race, for which the author obtained an average index for adults of 0.1. According to Martin (1914) the acromion lies even 8 to 10 mm. below the upper edge of the sternum in adult Europeans. It can be stated therefore that in adult whites in a normal position of rest the clavicles are either horizontally posed or point even downward with their lateral ends. In fetuses the clavicles diverge upward, deviating from a horizontal position in individual cases for as large an angle as 32° (see fig. 7). The adult Senois, negroes, and, judging by photographs alone, many other lower races remain in regard to the relative position of the shoulder closer to the fetal condition than whites. In adult apes and monkeys the shoulders are always situated relatively high (see table 8) and undergo practically no change during growth. It seems safe to conclude from these notes that the descent of the shoulders in man represents a comparatively new evolutionary experiment among primates, which has progressed farther in the higher than in the lower races. One might argue further than the height of the shoulder of the arboreal primates is directly connected with the fact that their upper limbs support part or all of the body weight and thus tend to pull or push the shoulders upward.

Table 8 shows that the orang, gibbon, and spider monkey, which swing by their arms, have actually the relatively highest

TABLE 8

Relative shoulder height (distance from middle of line connecting acromial points to suprasternal notch in percentage of anterior trunk height) during growth of whites and in adults of Senoi (calculated from data given by Martin, 1905), negroes, apes and monkeys

MAN			APES AND MONKEYS			
Age	Race	Average	Age	Primate	Minimum	Maximum
3rd month.....	White fetus	4.0	Adult	Orang-utan	13.8	
4th month.....	White fetus	7.0	Adult	Gibbon	12.0	
5th month.....	White fetus	6.9	Adult	Baboon	3.4	5.9
6th month.....	White fetus	6.6	Adult	Macaque	3.9	5.1
7th month.....	White fetus	5.7	Adult	Colobus monkey	3.7	4.6
8th month.....	White fetus	4.7	Adult	Proboscis monkey	7.9	
9th month.....	White fetus	4.8	Adult	Guenon monkey	4.8	9.0
10th month.....	White fetus	3.6	Adult	Patas monkey	3.8	4.1
Adult.....	White male	0.1	Adult	Capuchin monkey	4.6	10.0
Adult.....	Senoi male	2.7	Adult	Spider monkey	8.3	13.6
Adult.....	Negro male	3.0	Adult	Howler monkey	12.1	14.2

FIG. 7. WHITE FETUS OF THE 10TH WEEK SHOWING STEEPLY ASCENDING CLAVICLES (THE HEAD WAS OMITTED SINCE, IN ITS NATURAL POSITION, IT WOULD HAVE PARTLY OBSCURED THE CLAVICLES)

shoulders, while the lowest ones are found in the largely terrestrial baboons. The high indices of the howler monkeys are due to the fact that their suprasternal notch is situated abnormally low in consequence of the greatly enlarged hyoid capsule and of the forking in the manubrium sterni.

In relation to the spine the shoulders descend during human growth even more markedly than in relation to the upper edge of the sternum. While the latter moves only from the level of the seventh cervical vertebra in early fetal life to that of the second thoracic vertebra in adult life (see also Todd, 1912), the shoulder, respectively the highest point of the scapula, sinks according to Wolf (1925) from the level of the 4th cervical vertebra in a young fetus (18.5 mm. sitting height) to that of the fourth thoracic vertebra in adults.

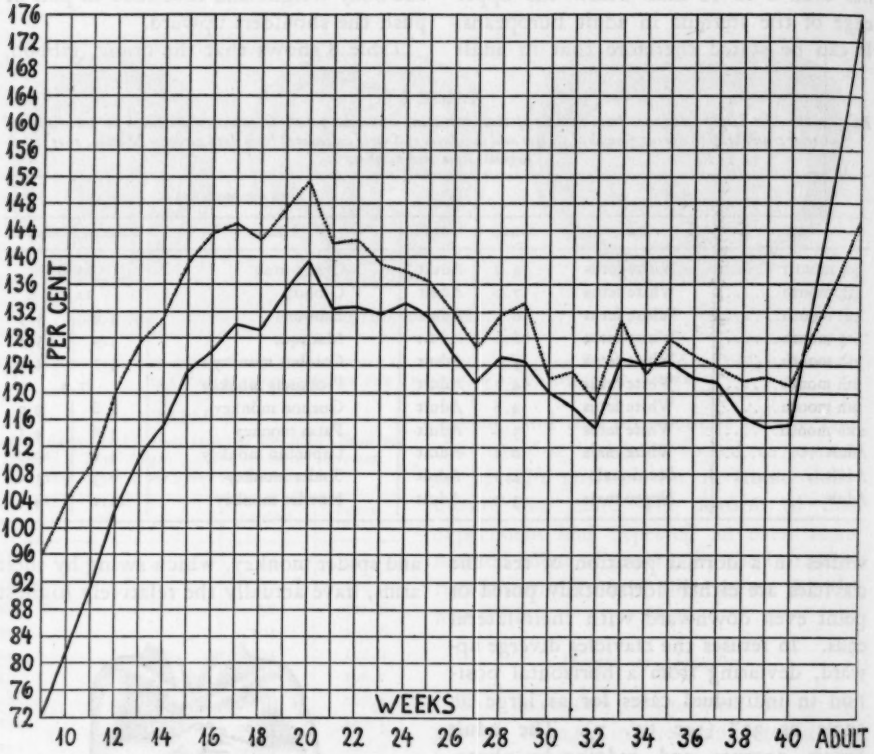

FIG. 8. CURVES OF GROWTH IN WHITE FETUSES AND ADULTS FOR THE PROPORTIONS: TOTAL LENGTH OF UPPER LIMB IN PERCENTAGE OF ANTERIOR TRUNK HEIGHT (DOTTED LINE) AND TOTAL LENGTH OF LOWER LIMB IN PERCENTAGE OF ANTERIOR TRUNK HEIGHT (SOLID LINE)

V. LIMBS

Total lengths of limbs in relation to trunk height

The relation in length between the extremities and the trunk changes very markedly in the course of growth. As

shown by the curves in figure 8, at 9 weeks of human fetal life both the upper and the lower limbs are still shorter than the trunk, but the latter increases at a slower rate than the former so that, at the end of the 5th month, the extremities greatly exceed the trunk in length. From then to birth the limbs grow more slowly than the stem, causing the relative limb lengths to decrease somewhat irregularly. During postnatal growth the limbs show again a greater growth rate than does the trunk, since the curves ascend a second time. These findings for fetal growth agree in principle with the results obtained by Reicher (1923), those for postnatal growth are in accord with the studies by Schwerz (1910), Weissenberg (1911), and others.

TABLE 9

Averages in white and negro fetuses and adults for the proportion: Total length of upper extremity in percentage of total length of lower extremity

AGE	WHITES	NEGROES	AGE	WHITES	NEGROES
9 weeks	132.7		26 weeks	104.8	109.2
10 weeks	126.8		27 weeks	104.2	108.1
11 weeks	119.8	123.1	28 weeks	105.3	107.4
12 weeks	116.6	121.3	29 weeks	106.8	106.7
13 weeks	115.8	118.3	30 weeks	101.4	102.9
14 weeks	114.1	114.7	31 weeks	104.5	105.5
15 weeks	112.8	116.1	32 weeks	103.4	107.1
16 weeks	113.2	113.9	33 weeks	104.5	104.5
17 weeks	111.6	113.2	34 weeks	99.3	104.5
18 weeks	110.5	112.2	35 weeks	103.6	106.5
19 weeks	108.7	109.1	36 weeks	103.3	106.6
20 weeks	108.2	109.7	37 weeks	102.1	104.6
21 weeks	107.4	112.7	38 weeks	104.9	106.7
22 weeks	107.0	107.6	39 weeks	105.9	104.4
23 weeks	105.6	108.0	40 weeks	104.9	102.7
24 weeks	103.8	106.4	Adults	82.5	83.4
25 weeks	104.2	105.4			

Relation in length between upper and lower limb

At the beginning of fetal development the arm length is very much greater (about one third) than the length of the lower limb, but with advancing age the two curves in figure 8 approach one another more and more until, soon after birth, they cross, when the leg becomes longer than the arm. This direct relation between the lengths of the upper and lower limb is clearly expressed in the so-called intermembral index, which is listed in table 9. This index decreases from the 3rd to the 6th month of fetal life, remains about constant from then to birth, to drop again in postnatal life. In general these growth changes bear out those obtained by Retzius (1904), Weissenberg (1911), and Reicher (1923); the actual sizes of the indices are somewhat at variance, mostly on account of differences in the method of measuring and calculating the proportion. The figures in table 9 permit the conclusion that negroes have somewhat longer upper limbs, in proportion to the lower ones, than whites and this not only at completion of growth but already in fetal life. The only apparent exception to this—immediately before birth—can not be regarded as very significant, since those averages are based upon small series of specimens only. In regard to this particular proportion the negro has gone not quite as far in a peculiarly human specialization as the white. Relatively long arms and short legs, resulting in a high intermembral index, are decidedly simian characters, whereas the reversed relation is typical for man, the only primate in which the index drops considerably below 100 in adult life. These facts are demonstrated by a comparison of tables 9 and 10. It is very noteworthy that this index undergoes a much more profound ontogenetic change in man (a decrease of about 50 units) than in any other primate; in the gibbon, e.g., it decreases for not more than 20 units and in the howler

monkey about 26 units. The tremendous difference in this proportion between various adult primates is not yet nearly as marked in fetal stages of development. For instance, in the adult gibbon the intermembral index amounts to as much as 159.1, which is 77 units above the value for adult white man; on the other hand, in a gibbon fetus, corresponding to a human fetus of the 3rd month, the index is as low as 157.6, which surpasses the average for 3 months old white fetuses by only 34 units.

The differences in the relative lengths of the limbs among adults of the higher primates are at once apparent in the diagrams of the frontispiece to this paper. Whereas in the apes the upper limbs are greatly lengthened, in man it is the lower limb which shows, indeed, a unique development. In relation to the trunk height the total length of the lower extremity is far greater in adult man than in any other adult primates. In regard to his relative upper limb length adult man occupies an intermediate and conservative position. This latter proportion amounts on a rough average to 145 in man, to 188 in gorilla (Mollison, 1911), and to 248 in the gibbon (*Hylobates lar* 230.8; *H. agilis* 232.3; *H. concolor* 280.0). In monkeys this relative upper limb length is, as a rule, markedly shorter than in man, except in such highly specialized forms as the spider monkeys (*Ateles geoffroyi* 176.1, 207.0, and 244.5; *A. paniscus* 187.8; *A. neglectus* 235.5) and some woolly monkeys (*Lagothrix infumata* 167.1). During individual development these different specializations in man and anthropoid apes make their appearance at quite different periods. As shown in the frontispiece, the extreme arm length of apes is already well defined in early fetal life; on the other hand, the unequalled length of the lower limb, characteristic of adult man, is not yet even indicated in intrauterine life, several of the ape fetuses surpassing the human fetus in this respect. Even at birth man has still proportionately short lower extremities, namely in percentage of the trunk height on an average in whites 115.7, as compared with 175.4 in white adults. In this, man resembles very closely the growth changes in the jumping mouse, in which the posterior limbs have also become greatly lengthened. In newborn jumping mice, just as in the human baby, this extreme condition is not yet apparent (Tschulok, 1922).

TABLE 10

Growth changes in apes and monkeys in the proportion: Total length of upper extremity in percentage of total length of lower extremity. The figures for gorilla and some of those for chimpanzee have been obtained from data in the literature. The fetuses in a perpendicular column correspond in their development approximately to human fetuses of the age stated at the top of the particular column

PRIMATE	AGE					
	Prenatal (month)			Postnatal		
	3rd	4th–6th	7th–10th	Infant	Juvenile	Adult
Gorilla		155.8				146.7
Chimpanzee		147.7	138.1	147.7–137.9	145.5	149.3–136.3
Orang-utan		181.1	174.3–171.7	178.9–172.1	175.2–170.1	166.7
Gibbon	173.4–157.6	157.8–155.8	161.2–156.3	155.6–150.3	165.0–150.7	159.1–153.5
Baboon		136.8–128.1	128.1–127.4	126.6	114.7–110.4	113.6–113.3
Macaque		131.8	127.2–126.2	126.4–124.4	122.9–114.6	119.2–107.8
Capuchin monkey		128.0	130.5	120.5	114.7–108.2	106.3–104.3
Howler monkey	149.2–146.0	144.5–136.4	138.1–137.3	139.5–133.3	130.7–124.8	130.6–122.7

It is not to be doubted that the ancestors of these specialized rodents once possessed shorter posterior limbs, and that, therefore, their ontogeny repeats their phylogeny in this respect. To be consistent, one now has to conclude that the corresponding late growth change in man also points to relatively shorter legs in human ancestors. One is tempted to argue further from the ontogenetically much later appearance of the unique human leg length than of the characteristic arm length of the apes, that the latter specialization was phylogenetically much earlier acquired than the peculiarity of man. However, this last assumption is offered merely as a suggestion, which needs support from additional investigations.

Relations in length between the proximal and middle segments of the limbs

The proportions between the length of the proximal and middle segments of the limbs undergo some changes during growth, which are shown in a condensed form by table 11. Both, the upper arm-forearm index and the thigh-leg index increase with advancing age, particularly up to the 5th fetal month and again in postnatal life. These findings, which are based upon a material of 623 fetuses, are not in agreement with the results of some other authors. Based upon a study of 22 specimens Hamy (1872) claims that the upper arm-forearm index of fetuses is higher than that of adults. The same conclusion was reached by Mendes Corréa (1919), who had measured only 10 specimens and used the data by Serrano (1895) on 6 additional ones. According to the former author the thigh-leg index also decreases with advancing age. Nishizuka (1925) found no uniform growth change in these proportions in Japanese; the following averages show this clearly: humero-radial index in fetuses of the 4th month (10 specimens) 73.6, in newborns (10 specimens) 74.1, in children (5 individuals) 69.1, and in adults (20 individuals) 71.5; femoro-tibial index at the same growth stages 74.7, 76.3, 76.4, and 75.9 respectively. Reicher's (1925) investigations on over 500 white fetuses revealed the following growth changes: The upper arm-forearm index rises from 76 at 9 weeks of fetal life to 79 at 10 weeks, during the 4th month it drops to 78, but rises again to 81 in the 5th month, fluctuating from then to birth between the averages of 80 and 81.5. The thigh-leg index increases from 78.5 in the 9th week to 85.5 in the 5th month, afterwards the averages decrease again to 84.5 in the 7th to 9th months, and to 81.5 in newborns. Even in regard to the postnatal changes in these indices no agreement has been reached as yet. For instance, Godin (1910), like the writer, finds the upper arm-forearm index to increase with age, namely, from 77 at 13 years to 83 at 17 years. Schwerz (1910), in contrast to this, obtains a

TABLE 11

Upper arm—forearm and thigh—leg proportion in white and negro fetuses and adults

AGE	FOREARM / UPPER ARM × 100		LEG / THIGH × 100	
	Whites	Negros	Whites	Negros
3 months, 1st half	72.9		66.7	
3 months, 2nd half	73.6	73.6	69.2	69.3
4 months	74.6	75.8	75.5	75.7
5 months	77.7	78.9	79.9	80.8
6 months	77.9	79.4	81.3	81.9
7 months	78.0	79.5	80.9	82.6
8 months	78.0	81.2	79.0	81.3
9 months	79.2	81.9	79.0	82.2
10 months	79.2	80.5	79.0	80.5
Adult males	83.6	91.4	84.1	84.9

decrease from 82.6 at 7 years to 78.1 at 20 years. The discrepancies in these results can not be entirely due to differences in the material under investigation but are, undoubtedly, to be accounted for to a very considerable extent by differences in the technique employed. The particular findings of the writer in regard to the growth changes in whites agree in principle very well with those obtained for negroes and are further supported by the analogous changes in other primates, as shown by the examples in table 12 and by those contained in a former paper by the author (1924 b, table 4). In a pregnant rhesus monkey, received recently, the upper arm-forearm index amounted to 96.5, whereas in the fetus (sitting height 163 mm.) of this specimen to only 90.5.

TABLE 12

Growth changes in the upper arm-forearm and thigh-leg proportions of the gibbon and of the spider monkey. The specimens are listed according to increase in body size

GIBBON (HYLOBATES PILEATUS)				SPIDER MONKEY (ATELES GEOFFROYI)			
Age	Sitting height	Forearm : upper arm	Leg : thigh	Age	Sitting height	Forearm : upper arm	Leg : thigh
	mm.				*mm.*		
Fetus	83	87.2	79.1	Fetus	178	87.0	93.9
Fetus	102	92.5	79.8	Fetus	187	89.3	93.0
Fetus	158	98.3	80.8	Newborn	191	87.7	90.6
Fetus	169	99.2	85.5	Newborn	195	88.8	90.0
Newborn	198	101.1	86.5	Infant	201	90.6	91.7
Juvenile		102.2	90.1	Infant	204	90.4	92.4
Juvenile		105.1	89.4	Infant	232	92.3	94.3
Adult		111.2	89.2	Juvenile		96.1	91.1
Adult		109.7	88.7	Juvenile		100.0	95.0
Adult		108.3	88.7	Juvenile		100.5	89.9
Adult		112.1	89.3	Adult		99.0	91.3
Adult		114.3	89.6	Adult		102.2	92.5
Adult		112.1	91.0	Adult		100.9	91.7

Among adult primates man possesses one of the relatively shortest forearms. Some of the primitive marmosets equal the human upper arm-forearm index (*Callithrix jacchus* 82.6 and 84.8, *C. penicillata* 84.8, *Leontocebus geoffroyi* 80.5 and 84.4). Of the higher primates gorilla alone rivals man in this respect (humero-radial index in 2 gorilla skeletons, Hopkins collection: ad. ♂ 78.9, ad. ♀ 78.2). In a large variety of other primates the forearm exceeds the upper arm in length, for instance, in a few individual chimpanzees and orangs (Sonntag, 1924), in all gibbons, and in most baboons and spider monkeys. Inasmuch as the forearm is proportionately shorter in fetuses than in adults, and particularly since an extreme length of the forearm, surpassing that of the upper arm, is found only in late ontogenetic stages (see table 12), it seems justifiable to assume that man and gorilla are conservative and primal in this proportion, whereas such forms as the gibbon have a highly specialized forearm.

In regard to the thigh-leg proportion, adult man is very similar to gorilla and chimpanzee, but has considerably lower values than the large majority of the lower monkeys. In some of the latter, as for instance in the spider monkey (table 12), this index does not increase with advancing growth.

It is of special interest to note that the

averages of both the indices, listed in table 11, are larger in negroes than in whites, and this in fetal as well as in adult life. This might be interpreted on the basis of the above discussion as indicating that these particular limb proportions have phylogenetically been even less modified in the white than in the negro. In the latter race they tended slightly in the direction which is typical of monkeys. The writer's studies on the ontogeny of primates have led him to disagree with the assumption of Mollison (1911) that the humero-radial and femoro-tibial indices of man have decreased in the course of evolution; he is inclined rather to the belief that these proportions have, if at all, become but little altered. The only direct evidence, available so far, would certainly support the author's view, since these indices are rather low in Neanderthal man (skeleton of La Ferrasie:

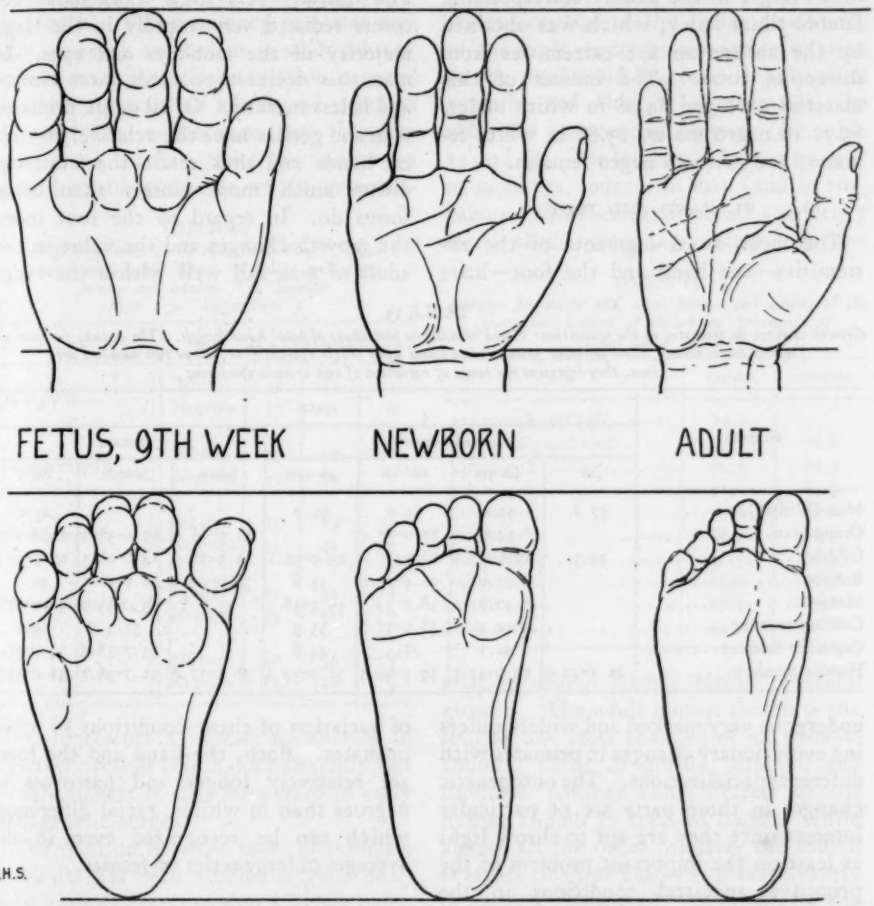

FIG. 9. DIAGRAMS ILLUSTRATING THE GROWTH CHANGES IN THE HUMAN (WHITE) HAND AND FOOT

humero-radial index 73.8, femoro-tibial index 76.6, Boule, 1911–13).

The racial difference in the thigh-leg index, derived from living adults, happens to be rather small. This difference was much larger in the closely corresponding femoro-tibial index, which was obtained by the author on 270 extremities from dissecting rooms. The indices of this material averaged 84.06 in white males, 85.71 in negro males, 83.88 in white females, and 86.10 in negro females.

VI. HAND AND FOOT

The most distal segments of the extremities—the hand and the foot—have undergone very marked and widely differing evolutionary changes in primates with different specializations. The ontogenetic changes in these parts are of particular interest since they are apt to throw light at least on the important problem of the primitive ancestral conditions in the original primate hand and foot.

Relative width of hand and foot

The hand as well as the foot becomes relatively narrower with advancing growth, as shown by figures 9 and 13 and by table 13. That the relative width of the hand and of the foot in monkeys equals that of man at early stages of development, i.e., about the time of the separation of the digits, is demonstrated by the illustrations of Keibel (1906). The initially very high hand index becomes reduced very rapidly in the large majority of the monkeys and apes. In man this decrease proceeds more slowly and is less marked. Of all adult primates man and gorilla have the relatively broadest hands and thus retain the fetal condition much more closely than other forms do. In regard to the foot index the growth changes and the value in the adult of man fall well within the range of variation of these conditions in other primates. Both, the hand and the foot, are relatively longer and narrower in negroes than in whites, racial differences which can be recognized even in the averages of large series of fetuses.

TABLE 13

Growth changes in primates in the proportion: Hand breadth in percentage of total hand length. The indices for man are approximate means, those for other primates are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th–5th	6th–8th	9th–10th	Infant	Juvenile	Adult
Man (Whites)	57.8	53.0	53.0	52.7			45.0
Orang-utan		34.0	37.0–37.4		31.5–36.8	29.2–38.2	22.0–28.1
Gibbon	34.5	29.6–37.4	29.2–31.0	29.0–32.2	23.5–32.5	24.1–26.5	21.7–25.0
Baboon		47.0	42.4–45.0	43.8	36.0–40.8	38.5–41.5	42.0
Macaque		40.8	38.7–39.3	36.5–38.5	35.7	35.0–35.9	32.0–33.3
Colobus monkey		41.4	38.0–38.7	35.3		31.5	29.1
Capuchin monkey		42.1	43.5	44.8		35.7–38.5	34.0–38.9
Howler monkey	42.1–42.9	39.9–45.2	39.5–40.5	38.0–39.2	36.5–37.8	32.7–36.2	31.0–33.9

Fingers

The middle finger is the longest of all fingers in all the primates and at any stage of growth, with the single exception of some prosimiae, in which the fourth finger may be the longest (at least in adults). In all primates the fourth finger

extends farther than the second finger, but this rule has also its exception, though this time it is found in man. According to table 14, white fetuses of the third month have in 2 percent of the cases the index finger surpassing the ring finger in length. This frequency increases rapidly, to reach 23 percent in adult whites. In negroes this particular relation is found in only 3 percent of adults and never in fetuses. The white race has therefore progressed farther than the negro in regard to this condition which, undoubtedly, represents a human peculiarity of relatively recent origin, and certainly one which at best is still very rare in early ontogenetic stages.

TABLE 14

Percentage frequencies of the relation in length between the second and fourth finger in white and negro fetuses and adults. (<"smaller than", > "larger than")

AGE	RACE	II < IV	II = IV	II > IV
3rd month	Whites	33	65	2
	Negroes	57	43	0
4th–5th month	Whites	15	67	18
	Negroes	49	51	0
6th–8th month	Whites	17	69	14
	Negroes	51	49	0
9th–10th month	Whites	32	54	14
	Negroes	59	41	0
Adults	Whites	18	59	23
	Negroes	55	42	3

The relation between these two fingers in adults has been studied a good deal, most authors agreeing that a longer index finger is more frequent in women than in men, much more frequent in whites than in negroes, and among the former most frequent in jews (Ecker, 1875; Mantegazza, 1877; Grüning, 1885; Weissenberg, 1895; Féré, 1900; Daffner, 1902). Among adult male Indians the author (1926) found a longer index finger in only 3 percent of the cases, i.e., in the same frequency as in adult male negroes.

Thumb

The thumb, when measured from the styloid process of the radius to the tip of the digit, becomes shorter in relation to the total hand length with advancing growth, and this in all primates. In man this ontogenetic decrease (see table 15 and fig. 9) is less marked than in apes or monkeys, indeed, in man (and in the baboon) there seems to prevail a tendency for a slight secondary increase in the relative thumb length during postnatal growth. The adult human thumb is the longest and least changed of all primate thumbs; those of gorilla, baboon, and capuchin monkey come nearest to the human thumb in relative length, while among all the other primates the thumb is either short or has even become nearly or entirely eliminated. Examples for the latter tendency are shown in figure 10. In many species of the African Colobus monkeys a free thumb has disappeared completely in adults; in fetuses, however, this digit is still fairly well developed (fig. 10, No. 1). Sir Harry Johnston (1904), speaking of the species *Colobus*

TABLE 15

Averages for white and negro fetuses and adults of the proportion: Length of thumb in percentage of total hand length

AGE	WHITES	NEGROES
3rd month, 1st half	74.0	
3rd month, 2nd half	74.7	71.6
4th month	72.9	69.9
5th month	71.1	69.9
6th month	70.4	67.2
7th month	68.7	66.7
8th month	67.9	66.5
9th month	68.0	65.9
10th month	67.7	65.8
Adult males	69.2	66.8

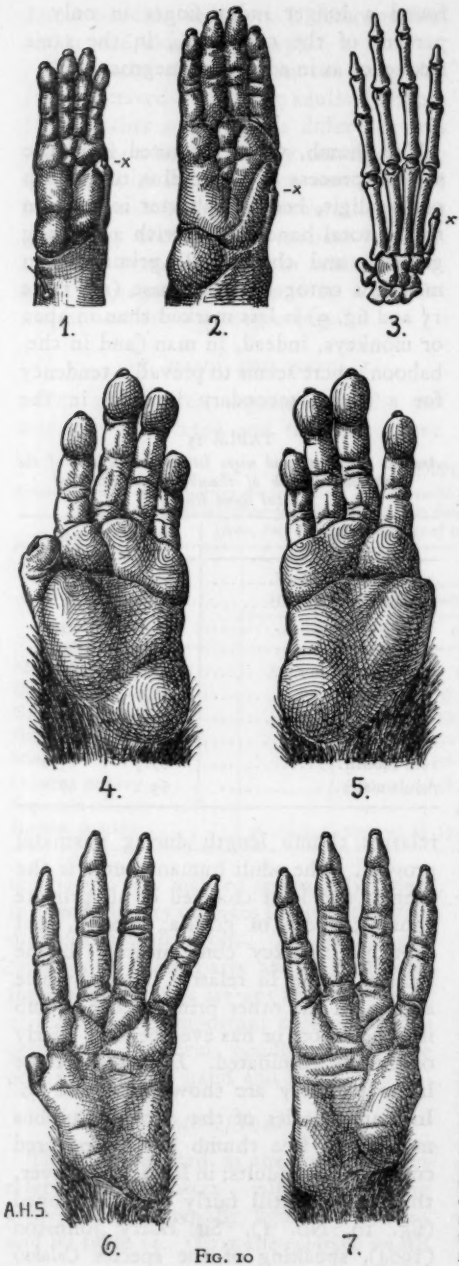

FIG. 10

tephrosceles, mentions that there is only "the minutest trace of a thumb nail in the place where the thumb is missing . . . . but the young Colobuses of this species have a complete thumb only a little smaller than this finger would be in the *Cercopitheci*. As the animal grows to maturity, so its thumb dwindles, until in a very old male there may be absolutely no trace left of the missing finger." In all the Guenon monkeys the thumb is very small and can be of but little use. In one specimen, recently obtained by the author, the free thumb was entirely missing on one hand (fig. 10, No. 5); that this was not due to any injury is proved by the fact that there is absolutely no trace of any scar formation. This hand represents a progressive variation, foreshadowing the future fate of the Guenon hand, just as the atavistic re-appearance of a free thumb on the hand of an occasional spider monkey (fig. 10, No. 6) is the individual reversion to an ancestral condition. Among 58 spider monkeys the author found two in which the thumb was still present on one hand only.

From these notes it can be concluded that among the arboreal primates there exists a wide-spread tendency toward the elimination of the first finger—a specialization which reaches its extreme only at completion of growth and which varies

FIG. 10. EXAMPLES SHOWING THE TENDENCY AMONG PRIMATES TO REDUCE THE THUMB

Nos. 1, 2, and 3 hands of Colobus monkey (*Colobus abyssinicus ituricus*), rudimentary thumb at x; No. 1 fetus (112 mm. sitting height), No. 2 older fetus (134 mm. sitting height), No. 3 adult female (metacarpus and one phalanx of thumb still present but proportionately very small and not visible on outer hand). Nos. 4 and 5 left and right hand of adult male Guenon monkey (*Lasiopyga pygerythra*), left thumb of typical size for these particular monkeys, right thumb congenitally missing on the outer hand (metacarpus I present but small). Nos. 6 and 7 left and right hand of infantile female Spider monkey (*Ateles geoffroyi*); the complete lack of an outer thumb is normal for Spider monkeys, but on the left hand of this specimen the thumb is still present, containing a well developed metacarpus and two fused phalanges.

individually to a considerable extent. This evolutionary trend has not affected man, whose thumb has changed but little from the relative length, typical of all young primate fetuses.

The racial difference in this proportion, according to which the negroes have at all ages a considerably shorter thumb than whites (table 15), marks the former as slightly more "simian" in this respect, and, as it happens, the white as even more original or "primitive."

In early fetal life the free thumb branches from the palm immediately at the base of the index finger. In the course of growth this place of branching shifts proximally to a place nearer the wrist (see fig. 9). This ontogenetic migration is most pronounced in orang-utan and gibbon, somewhat less in other anthropoids and man, as well as in most Old World monkeys, while in the large majority of the American monkeys no such shifting takes place at all, the thumb persisting in its typically fetal position throughout life. This movement of the thumb, away from the other fingers, in the catarrhine hand has greatly facilitated the opposability of the thumb. In platyrrhines this digit is either not opposable at all, as in the marmosets, or, as in the *Cebidae*, only to a much lesser degree than in the African and Asiatic primates. The opposability of the thumb, which was and is of greatest importance for the evolution of man, was not yet a feature of the original primate hand. It is significant, but not surprising, therefore, to find that this condition is still lacking in the human embryo. Not only does the embryonic thumb branch at a place unfavorable for effective opposability but it is not yet rotated around its longitudinal axis to face the other digits, as is clearly shown by the diagrams in figure 11.

FIG. 11. FETAL AND ADULT HAND OF MAN, SEEN FROM IN FRONT, SHOWING THE ROTATION OF THE THUMB
The straight lines run parallel to the transverse axes of the finger nails

Toes

Among primates the middle toe reaches, as a rule, farther than any of the other toes. Exceptions to this are found among the lemurs and marmosets, in which the fourth toe often equals the third in length, or, in rarer cases, may even surpass it (e.g., in one out of 8 marmosets of the author's collection). The only other exception is man, in whom the second or even the first toe has become the longest. It is very interesting that early in ontogeny man still shows occasionally the typical digital formula of his simian relatives, since in 4 to 5 percent of human fetuses from the beginning of the 3rd month the middle toe is the longest (fig. 12). In very rare instances this, for man undoubtedly primitive, condition may even persist to adult life; Wood Jones (1920) mentions two such cases and Hawkes (1914) found it in 19 persons. Table 16 demonstrates the gradual changes during human growth in the relations in length between the toes. In the beginning of fetal life the great toe is never

longer than the second toe, but the reversed relation occurs in 98 percent of whites. On the other hand, in adult whites the second toe is the longest in only 12 percent of the cases, while the great toe has surpassed the others in 52 percent. The latter condition is, phylogenetically speaking, a relatively new and exclusive acquisition of man. In the white race it is found with much greater frequency than in the negro, who has remained in this point somewhat less specialized than the average white, and who certainly tends to retain the fetal condition more closely.

FIG. 12. FRONT VIEW OF A HUMAN FETUS (25 MM. SITTING HEIGHT) WITH MIDDLE TOE LONGER THAN THE OTHER TOES
Note also the short and abduced great toes

There exists a considerable literature on the relative length of the first two toes of adult man, a large part of it centering on a sex difference in this feature. How uncertain, however, such a sex difference must be, is evident from the conflicting results. For instance, Harrison (1884), Daffner (1902), and Hawkes (1914) find a longer second toe more frequently in women than in men, Grüning (1885) maintains just the opposite, while Weissenberg (1895) claims that there is no difference in the two sexes. According to Maurel (1888) the second toe surpasses the first in length more frequently in Mongolian races than in whites or negroes.

In man the distance from the heel to the tip of the great toe increases with advance in growth faster than the foot length, measured to the tip of the middle toe. This relation is just the opposite in monkeys and apes, i.e., the great toe becomes relatively shorter. This is illustrated by figure 10 and, especially, by figure 13. The latter figure also shows

TABLE 16
Percentage frequencies of the different relations in length between the the first three toes in white and negro fetuses and adults

AGE	RACE	DIGITAL FORMULA I ∧ II ∧ III	I ∧ II = III	I ∧ II < III	I = II < III	I < II < III
3rd month	White	4	6	88	2	0
	Negro	5	5	95	0	0
4th–5th month	White	0	0	40	44	16
	Negro	0	2	81	12	5
6th–8th month	White	0	0	28	34	38
	Negro	0	0	43	42	15
9th–10th month	White	0	0	11	31	58
	Negro	0	0	39	38	23
Adults	White	0	0	12	36	52
	Negro	0	0	39	40	21

that the phalangeal portions of the lateral toes (II to V) are, in regard to their relative lengths, little different in the fetuses of man and monkey. But, while these digits have become relatively shorter in adult man, they have increased their proportionate length tremendously in the adult monkey. This leads to the conclusion that even such widely different types of feet as those of man, with their extremely short lateral toes, and those of the howler monkey, in which these toes

are excessively developed, can ontogenetically be traced to very similar forms, from which the different specializations cause them to grow in opposite ways, whereby the monkey foot changes more profoundly than the human foot.

Gorilla may be an exception to the rule stated above that the great toe becomes relatively shorter in monkeys and apes, but the different species of this ape vary considerably in this respect. The following values for the relative length of the great toe in gorilla were chiefly obtained from measurements on plaster casts and on illustrations and are therefore only approximate: fetus (Duckworth, 1904) 82.1; older fetus (Deniker, 1885) 87.2; 3 year old female (cast of foot of "Dinah," lent by Dr. McGregor) 74.3; 3½ year old male ("John Daniel II," measured alive by the author) 83.8; 5 year old male (cast of foot of "John Daniel I," donated by Dr. McGregor) 82.2; adult female (cast of foot by Mr. Akeley, donated by Amer. Museum of Natural History) 91.6; adult (Hartmann, 1880) 85.1.

For chimpanzee the following figures are available: newborn (preserved specimen, lent by Dr. Huntington) 86.3; infant (preserved specimen, lent by U. S. National Museum) 85.1; adult (Beddard, 1893) 74.2; several other adults (from various photographs) 78–85; adult male (cast by C. H. Ward) 89.5.

In orang-utan the index was found to average 62.5 in 3 fetuses of an advanced state of development, 59.4 in 5 infantile (preserved) specimens, and 52.1 in 2 adults (casts).

In man this index (foot length to 3rd toe!) amounts to about 95 in fetuses of the 3rd month and in adults it varies between 98.5 and 108.5.

In all primate embryos the great toe, just after its appearance on the foot plate, is found to branch from the sole very close to the base of the second toe. In

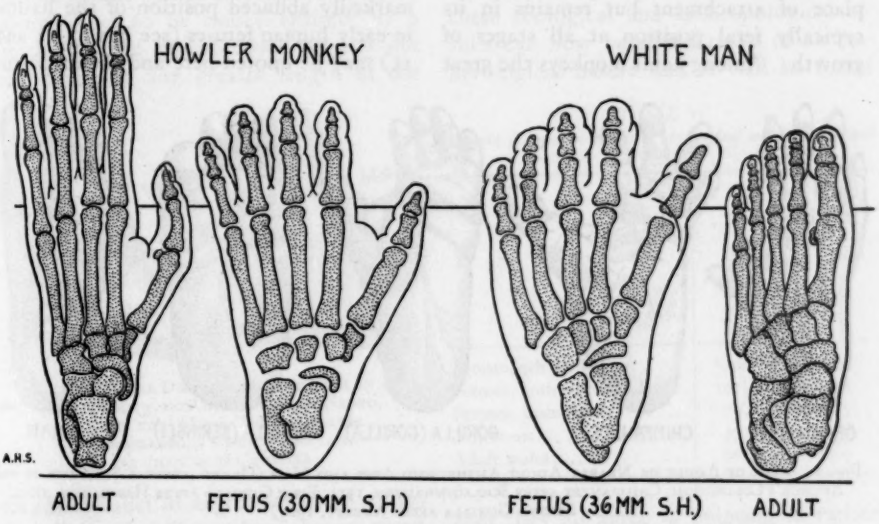

FIG. 13. DIAGRAMS OF THE GROWTH CHANGES IN THE FOOT OF MAN AND OF A MONKEY (*Alouatta seniculus macconnelli*)

The four feet are reduced to the same distance from the heel to the second metatarso-phalangeal joint.

all monkeys and apes this place of branching shifts proximally in the course of growth, toward a place nearer the ankle, just as the thumb moves ontogenetically away from the base of the index finger. However, both these rules have their exceptions: For the thumb it exists, as discussed above, in most of the platyrrhine monkeys, which retain the fetal condition to adult life; in regard to the great toe it is man, who behaves in an exceptional way, since his great toe does not shift its place of attachment but remains in its typically fetal position at all stages of growth. Among adult monkeys the great toe branches from the sole at a varying but always considerable distance from the base of the second toe (see e.g., Pocock, 1926). Among adult anthropoid apes this feature differs least from the human condition in the mountain gorilla, and most in orang-utan, with a greater discrepancy between the latter two than between gorilla and man (see figure 14). There can be no question that the opposability of the great toe is greatly facilitated by its branching at a place which is removed from the second toe, so that, in the act of grasping, these toes together with the intermediate medial edge of the sole form diagrammatically a U, rather than a V, as in man. The degree of opposability of the hallux is much more perfect in orang and chimpanzee than in the adult East-African gorilla and, of course, than in man. There is some embryological evidence which can be claimed as support for the assumption that the human pedigree contains forms with an at least partly opposable great toe. The relatively short length and markedly abduced position of the hallux in early human fetuses (see figs. 9, 12 and 13) may be quoted here and then particularly the investigations of Straus (1927), who found a somewhat greater rotation in the sense of opposability in the first metatarsal of early human fetuses than in that of adult man.

FIG. 14. FEET OF ADULT OR NEARLY ADULT ANTHROPOID APES AND MAN (ORANG AFTER A SPECIMEN IN THE AUTHOR'S COLLECTION; CHIMPANZEE AFTER SCHLAGINHAUFEN, 1911; FIRST GORILLA AFTER HARTMANN, 1880; SECOND GORILLA AFTER AKELEY, 1923)

Heel

To this discussion on the foot must be added a few remarks concerning the heel. In all monkeys the profile of the heel forms a practically straight line running smoothly from the calf to where it bends over to the sole. Among the anthropoid apes, especially in gorilla, one encounters

for the first time indications of a prominent heel, i.e., a heel which projects beyond the profile of the ankle region. In human races the degree of prominence of the heel is much more developed in the negro than in the white; indeed, this forms a most striking racial difference even in fetuses. Negro fetuses from the 5th or 6th month to term can, as a rule, be readily identified by their characteristic heel. By dissecting a considerable number of white and negro heels in fetuses and in adults the author found the projecting heel to be caused entirely by a thick layer of subcutaneous fat and not to be due to any greater length of the

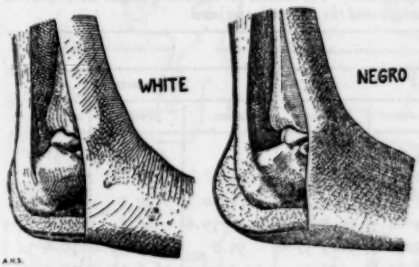

FIG. 15. PARTIAL DISSECTION OF THE HEEL IN AN ADULT WHITE AND IN AN ADULT NEGRO, SHOWING THE MUCH THICKER LAYER OF SUBCUTANEOUS TISSUE IN THE LATTER THAN IN THE FORMER

corpus calcanei in negroes than in whites (see fig. 15). The subcutaneous tissue in the heel region of monkeys is proportionately much less developed than in white man and does not extend far up on the tuber calcanei. Why the negro heel should be padded even to some distance above the tuber calcanei is difficult to understand. Underneath the heel this subcutaneous padding serves as a sort of shock absorber in walking.

VII. ANALOGIES IN THE GROWTH OF UPPER AND LOWER LIMB

Mollison (1911), in an excellent monograph on the body proportions of primates, has demonstrated that there exists a certain correlation between the size of corresponding parts of fore- and hind-limb in monkeys and apes, a condition which he called the homotypy of proportions. One instance suffices to illustrate this correlation: Primates with unusually long hands, such as orang-utan, also possess very long feet. P. and F. Sarasin (1892–93) had called attention to the fact that human races with a relatively long forearm have also a proportionately long leg and *vice versa*. To these zoological and anthropological results can now be added those of an embryological nature and it will be found

TABLE 17

Growth changes in whites in the leg-foot and forearm-hand proportion

AGE	$\frac{\text{FOOT LENGTH}}{\text{LEG LENGTH}} \times 100$	$\frac{\text{HAND LENGTH}}{\text{FOREARM LENGTH}} \times 100$
Fetuses, 9th week	139.2	118.4
Fetuses, 10th week	107.0	91.0
Fetuses, 15th week	79.1	71.3
Newborns	97.5	94.8
Adult males	68.7	74.9

that they all agree in pointing to rather close analogies, or a certain parallelism, in the phylogeny as well as the ontogeny of the upper and lower extremities.

The age changes in the relative lengths of the limbs, as illustrated by the curves in figure 8, show probably clearer than anything else the close correlation between upper and lower limb during growth. From table 11 it is evident that both the upper arm-forearm proportion and that between thigh and leg is altered between fetal and adult life in a very similar way and that both these corresponding indices are always larger in

negroes than in whites. A comparison between the leg-foot proportion (given in figure 3) with the relation in length between the corresponding parts of the upper limb, the forearm and hand (contained in figure 4) reveals the fact that the very striking growth changes in these proportions agree in principle very closely, since in both indices there occurs first a marked and rapid decrease, changing after the 15th week of fetal life into an increase, and after birth changing back again to a second decrease (see table 17). Finally, both the hand and the foot become relatively much narrower with advance in growth (see fig. 9) and both these parts are slightly narrower in negroes than in whites.

It is most likely directly due to this close analogy in the growth of the upper and lower limb that the proportion between these limbs (intermembral index) is very much more constant than the proportion between either of the two limb lengths and the trunk height. As a matter of fact, the intermembral index varies individually less than almost any other proportion on the body. This holds true in regard to fetuses as well as in regard to adults (see table 27).

VIII. HEAD

Relative size of brain part of head

It is a general and well established rule for vertebrates that in related animals the relative brain size decreases as the body size increases. This is sometimes referred to as Haller's law. Of the many authors, who have collected data in support of this rule, only a few may be mentioned here, namely Weber (1896), Dubois (1897, 1914), Brandt (1898), Hrdlička (1905, 1925 b), Lapicque (1909), and Funk (1911). A clear example for illustrating this relation between relative brain size and body size is found in a comparison between house cat and lion: Of the 3,300 grams body weight in the former the brain forms 0.94 per cent, while of the 119,500 grams body weight of the latter the brain constitutes only 0.18 per cent. Among primates it is also found that by and large the smaller the species the proportion-

TABLE 18

Growth changes in the relative head size (average head diameter in percentage of anterior trunk height) of primates. The indices for man are approximate means, those for apes and monkeys are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens. The indices for the chimpanzees were obtained from data by Friedenthal (1914), except those for the nearly newborn and the infantile specimen

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th–5th	6th–8th	9th–10th	Infant	Juvenile	Adult
Man (Whites)	85.0	78.0	69.0	59.0			31.0
Chimpanzee		59.8	60.4	49.5	39.0	34.6	28.5
Orang-utan		65.0	63.8–64.9	60.7	56.9–60.2	49.0	31.8
Gibbon	61.4–67.6	62.4–64.9	63.4–64.5	60.8–60.9	52.5–59.6	48.8	30.2–33.3
Baboon		55.0	57.5–51.3	56.3–57.0	55.7	38.3–39.8	30.6–34.5
Macaque		57.5	54.8–54.8	51.9	34.1–40.2	26.8–27.0	23.5–27.5
Proboscis monkey			48.9–50.3	44.0			18.5
Colobus monkey		49.7	49.6–51.4	47.3			20.1
Capuchin monkey		63.2	70.9		50.6	38.7–44.4	30.9
Howler monkey	67.7–73.3	59.6–62.6	54.6–57.5	49.1–54.3	46.2–49.0	30.2–37.7	26.6–27.1
Spider monkey				51.3–56.0	47.3–51.9	38.5–43.8	24.4–31.7

ately larger is the brain. The following figures (brain weight in percentage of body weight, calculated from data of Dubois, 1914) suffice to demonstrate this: orang-utan (73,500 grams) 0.54, gibbon (9,500 grams) 1.37, marmoset (335 grams) 3.82. The relative brain weight of adult man (white males 2.18) is surpassed by that of many small monkeys but is much higher than that of any of the large apes.

The influence of body size on the relative size of the brain is also noticed in part of the head decreases in all vertebrates as the individual grows to larger size. For instance, the arithmetic mean of head length, breadth, and height (head module), expressed in percentage of the trunk height, amounts on an average to 95.5 in human fetuses of the 9th week, but in adult man this proportion has decreased to 31.1. According to table 18, other primates show very similar changes. It is interesting to note that the decrease in this index may proceed during correspond-

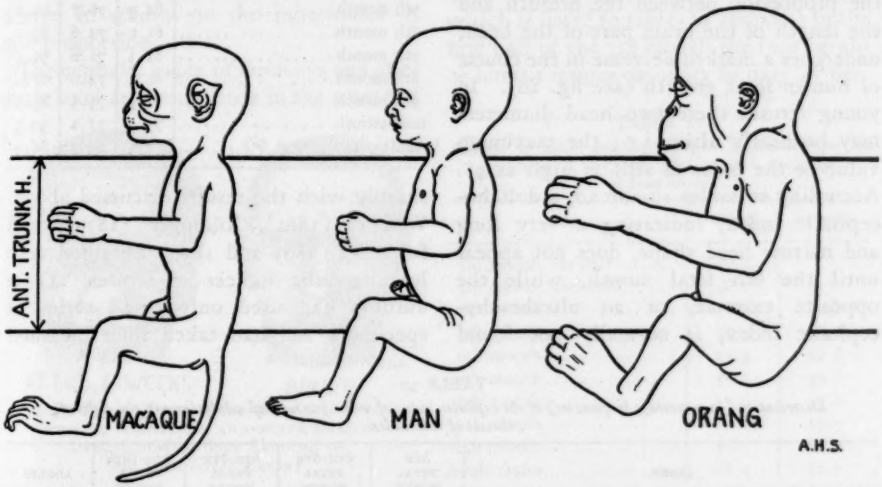

FIG. 16. BODY PROPORTIONS IN NEWBORN MACAQUE, MAN, AND ORANG-UTAN; ALL REDUCED TO THE SAME ANTERIOR TRUNK HEIGHT
Note the different sizes of the brain part of the head

the different human races, since pygmies have in general proportionately larger heads than the tall races. Indeed, it can even be demonstrated within a race, as was done for whites, e.g., by Hrdlička (1925 a) and for American Indians by the author (1926 a).

These introductory notes form a necessary background for the discussion of the growth changes in the relative head size, since it appears that the above rule may also be applied to the conditions of development. The relative size of the brain ing periods of development with different intensity in different primates. For instance, in the orang-utan and in the gibbon the prenatal decrease is very much smaller than in man, so that at birth these apes have a proportionately larger head than newborn babies. That the latter fall well within the range of variation of the relative head size among newborn monkeys and apes is also shown by figure 16.

In conclusion it may be stated that the large proportionate size of the brain part

of the head in primate fetuses, which is directly responsible for their high forehead, is of no phylogenetic significance. In other words, it can not support theories, such as have been advanced by Kollmann (1905), Klaatsch (1923), and Hill-Tout (1921, 1924), but is due to specific conditions of growth, common to all vertebrates.

Cephalic index

The cephalic index, which expresses the proportion between the breadth and the length of the brain part of the head, undergoes a marked decrease in the course of human fetal growth (see fig. 20). In young fetuses these two head diameters may be nearly alike, i.e., the maximum value of the index is still as high as 98. According to tables 19 and 20, a dolichocephalic index, indicating a very long and narrow head shape, does not appear until the 6th fetal month, while the opposite extreme, or an ultrabrachycephalic index, is normally not found after the 7th month of prenatal development. These results agree in principle with the findings of Retzius (1904). Mazzi (1918) found 71 per cent of 9 to 10 months old fetuses to be brachycephalic (average 84.3), a percentage which is even higher than that of the writer. Mazzi's further conclusion, that the cephalic index increases before the 9th fetal month, is of little significance since it was based upon observations on only 6 specimens. The older literature contains some reports which contrast sharply with the results discussed above. Welcker (1862), Rüdinger (1877), and Schaeffer (1893 and 1896) obtained very low cephalic indices in fetuses. These authors had used only small series of specimens and had taken their measurements on the skull which is easily distorted and shrinks in drying very considerably, hardly ever retaining its normal shape.

TABLE 19

Averages and ranges of variation of the cephalic index (head breadth in percentage of head length) in white fetuses and adults

AGE	AVERAGE	MINIMUM	MAXIMUM
3rd month, 1st half	87.4	81.6	98.0
3rd month, 2nd half	86.6	77.8	96.9
4th month	87.6	76.5	97.2
5th month	84.9	76.7	93.0
6th month	82.2	74.6	89.1
7th month	81.3	71.6	92.1
8th month	81.3	74.0	87.2
9th month	81.5	73.5	85.3
10th month	79.3	71.2	90.3
Adults (100 ♂ and ♀)	77.5	69.7	86.9

TABLE 20

Distribution (in percentage frequencies) of the cephalic index of white fetuses and adults among the different classes of this index

INDEX	3RD FETAL MONTH	4TH–5TH FETAL MONTH	6TH–7TH FETAL MONTH	8TH–10TH FETAL MONTH	ADULTS
Dolichocephalic, x–75.9	0	0	7	17	22
Mesocephalic, 76.0–80.9	10	12	31	32	57
Brachycephalic, 81.0–85.9	35	27	41	41	20
Hyperbrachycephalic, 86.0–90.9	32	47	20	10	1
Ultrabrachycephalic, 91.0–x	23	14	1	0	0

From the figures in tables 19 and 20 can be concluded that dolichocephalic adults must, as a rule, have changed more during their ontogeny in regard to head shape than broad-headed adults.

Among the latter the cephalic index may undergo a slight secondary increase after birth (e.g., Tschepourkovsky, 1911). Pfitzner (1899) found this index to remain constant from birth to adult life. It can be stated, however, that in general the head index decreases during postnatal growth, as was demonstrated on very large material for instance by Porter (1894), Hrdlička (1900), and Röse (1905). This occurrence of age changes in the cephalic index has not always been considered in studies on the inheritance of this proportion.

The cephalic index of monkeys and apes seems to change very little in the course of

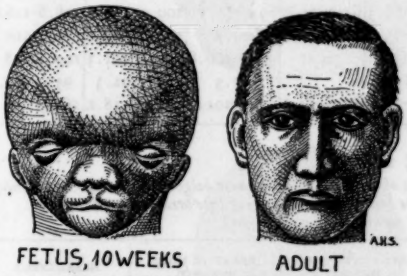

FIG. 17. FRONT VIEWS OF THE HEAD OF A HUMAN FETUS, 10 WEEKS OLD, AND OF THE HEAD OF AN ADULT MAN, BOTH REDUCED TO THE SAME TOTAL HEIGHT

growth. For instance, it ranges in gibbons between 82.5 and 90.1 in 11 fetuses, and between 84.1 and 90.8 in 7 adults. In very broad-headed monkeys the index tends even to increase with advance in age; e.g., the values for howler monkeys varied in fetuses (48 to 68 mm. sitting height) from 84.8 to 86.8 and in adults from 90.3 to 94.2.

The prenatal growth changes in the human cephalic index can not be interpreted as being of phylogenetic significance. It is much more likely that the intracranial pressure in the embryo tends to mold the soft brain part of the head into a sphere, from which approximate form the head can depart only after the skull has become more widely ossified.

Relative height of the face

The face part of the head grows faster than the brain part in man as well as in all the other primates (see fig. 17). This is most strikingly demonstrated by the so-called vertical cephalo-facial index or the proportion between the height of the face (to the naso-frontal suture) and the head height (from the ear opening), which is listed in tables 21 and 22. In the first half of the 3rd month the face height of human fetuses amounts to only 47 per-

TABLE 21

Averages of white and negro fetuses and adults for the proportion: Total face height in percentage of head height

AGE	WHITES	NEGROES
3rd month, 1st half	47.4	
3rd month, 2nd half	48.7	52.2
4th month	51.2	55.2
5th month	54.4	57.1
6th month	55.9	57.8
7th month	55.3	59.7
8th month	57.0	59.2
9th month	57.2	59.3
10th month	58.3	60.7
Adult males	85.4	91.7

cent of the head height, but in adult whites to 85 percent. In all adult monkeys and apes this index is very much higher than in adult man, rising with but few exceptions considerably above 100. The maximum index, of 172.6, was found in a male adult howler monkey, which surpasses the average adult white man by 87 index units. A howler monkey fetus, corresponding in development to human fetuses of the 11th week, differs from the latter by only 12 index units.

The growth changes in this proportion are much more marked after birth than during fetal life. This is chiefly due to

the comparatively late development of the masticatory apparatus, which increases the facial height tremenduously during childhood.

The figures in table 21 show a marked and constant racial difference, according to which negroes have the proportionately higher face, respectively lower

The face height of the negro is also slightly greater than that of the white in its relation to the face breadth, and this, too, in fetuses as well as in adults. This height-width proportion of the face (upper face height in percentage of face breadth) remains practically unaltered during fetal growth (approximate average in whites

TABLE 22

Growth changes in the proportion: Total face height in percentage of head height. The development, but not the actual age, of the different monkey fetuses in a given perpendicular column corresponds approximately to that of human fetuses of the stated age in the particular column

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th–5th	6th–8th	9th–10th	Infant	Juvenile	Adult
Orang-utan		75.6	83.6–86.2	91.4	87.4–91.0	108.3	127.7–150.0
Gibbon	53.8–61.1	63.1–64.8	60.5–66.3	64.5–65.4	69.0–75.7	100.0–101.1	108.8–126.7
Baboon		76.2	80.2–85.3	81.0	84.7	117.5–130.6	146.1–161.8
Macaque		64.1	68.5–71.0	74.0	94.9–106.8	101.9–121.3	124.4–158.0
Capuchin monkey		71.3	68.3		77.5	83.7–92.3	95.9–109.4
Howler monkey	60.6–63.0	77.6–79.5	77.6–89.4	81.8–84.5	91.5–101.3	115.7–128.2	162.7–171.6

TABLE 23

Averages of white and negro fetuses and adults for the proportions of the nose: Relative nose height (nose height in percentage of upper face height), Relative nose breadth (nose breadth in percentage of face breadth), and Nasal index (nose breadth in percentage of nose height)

AGE	RELATIVE NOSE HEIGHT		RELATIVE NOSE BREADTH		NASAL INDEX	
	White	Negro	White	Negro	White	Negro
3rd month, 1st half	63.8		34.8		137.6	
3rd month, 2nd half	70.2	66.8	31.0	35.6	115.3	130.2
4th month	68.5	64.1	26.8	30.3	105.9	121.0
5th month	68.5	64.8	24.6	27.9	97.8	121.1
6th month	67.5	64.9	25.1	28.4	98.4	108.8
7th month	67.3	63.0	25.2	28.4	97.8	109.8
8th month	68.0	61.2	25.5	29.3	97.6	114.7
9th month	67.1	61.6	24.2	28.3	97.3	114.4
10th month	66.0	63.1	24.2	28.1	95.9	111.0
Adult males	71.3	67.0	24.6	30.5	62.1	79.6

brain part of the head, than whites. This difference is already apparent in fetuses. Since man has the lowest index of all primates and whites even lower values than negroes, it can be stated that the white race has deviated farther from the simian condition of this proportion than has the negro.

39), but changes considerably in postnatal life (average in white adults 56), when the face grows much more intensely in height than in width.

Nose

The conditions of growth of the human nose are shown in a condensed form in

table 23. In both, whites and negroes, the nose becomes in general relatively higher and narrower with advancing development, and, in consequence of this, the nasal index decreases (see also fig. 17). In the 3rd month of fetal life 98 percent of the whites are hyperchamaerrhinic, i.e., have a nasal index above 100. In the 4th month 84 percent of the whites still fall into this group, but in whites of the 10th month only 46 percent have retained this high index. Among adult whites there are no chamaerrhinic individuals left at all, 96 percent of the cases being leptorrhinic, i.e., having a nasal index below 70. The nasal index, formed from measurements on the bony nose, also decreases during fetal growth, namely from 77 in the 3rd month to 62 at birth (Broca, 1872). The values of the latter index are much below those for the external nose on account of the difference between the nasal breadth and the width of the apertura piriformis, a difference which becomes steadily less with advancing growth (Schultz, 1918 & 1920). During postnatal life the height-width proportion of the external nose continues to decrease, as has been shown by many investigators, e.g., Houzé (1888), Blind (1890), and Schwerz (1910).

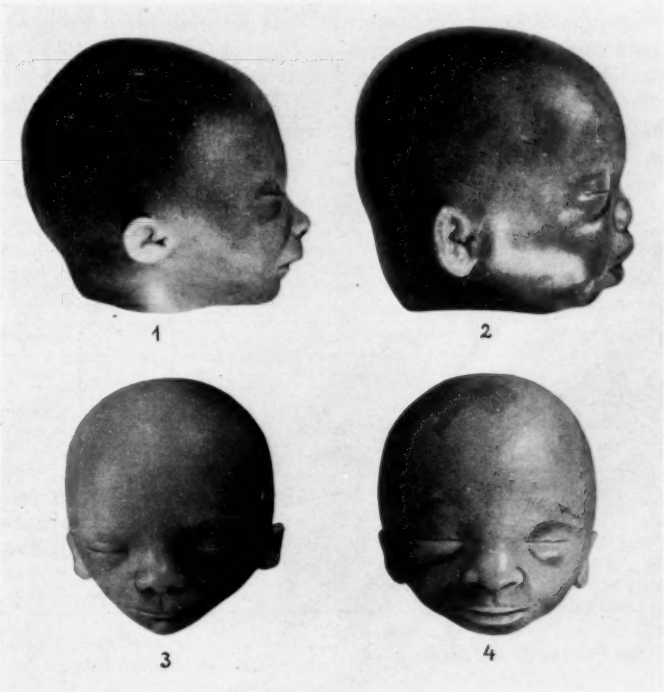

FIG. 18. RACIAL DIFFERENCES BETWEEN THE HEADS OF WHITE (NO . 1 AND 3) AND NEGRO (NOS. 2 AND 4) FETUSES
All four specimens about 5 months old. Note particularly the differences in the nose and in the lips

In monkeys and apes the nasal index decreases with advance in growth, as in man. embryos having a proportionately

very broad nose (see e.g., figures 16 c and 22 c by Keibel, 1906). However, the decrease of the nasal index occurs in most monkeys much more rapidly than in man, so that monkey fetuses have considerably lower indices than human fetuses. In the gibbon, for instance, the nasal index amounts to 62.8 in a fetus (56 mm. sitting height) and varies between 38.7 and 42.8 in adults. The nasal index of howler monkeys was found to be 80 in a fetus (48 mm. sitting height) and anywhere from 51.9 to 58.3 in adults.

The three proportions of the nose, listed in table 23, show at all growth stages very marked racial differences. In relation to the upper face height the nose is lower in the negro than in the white. This implies directly that the upper lip, as measured from the root of the nasal septum to the middle of the mouth, is relatively higher in the former race than in the latter. The nasal breadth, in its relation to the breadth of the face, is very much larger in negroes than in whites; even in fetuses is this racial difference unusually well marked (see fig. 18, Nos. 3 and 4; other illustrations were published by the author in 1920 and 1923a). The nasal index decreases ontogenetically to much lower values in whites than in negroes. The nose of the latter, therefore, is broader than that of the former not only in relation to the face breadth but also in proportion to the nose height. The nose of the adult negro has in every respect deviated less from the human fetal nose than has the adult white nose. The latter has advanced ontogenetically as well as phylogenetically to the highest development, whereas the nose in such races as the Australians and the Bushmen represents the most primitive and least specialized condition in man.

TABLE 24

Growth changes in the proportion: Interocular breadth in percentage of face breadth. The indices for man are approximate means, those for other primates are based upon single specimens or, where two numbers are given, they represent the range of variation of two or more specimens

PRIMATE	AGE						
	Prenatal (month)				Postnatal		
	3rd	4th–5th	6th–8th	9th–10th	Infant	Juvenile	Adult
Man (Whites)	44.0	32.0	27.5	25.0		24.3	23.0
Orang-utan		29.3	15.4–18.5	19.1	11.8–18.7	12.2–20.1	12.0
Gibbon	65.7–34.0	25.7–30.0	23.4–28.5	24.4–26.5	20.7–25.6	20.4–23.8	18.6–27.2
Baboon		26.8	19.0–20.9	18.0–18.3	15.3–15.6	12.5–15.1	17.9
Macaque		21.3	18.0–24.1	21.5	15.9–21.5	12.3–16.7	15.1–15.6
Colobus monkey		25.2	22.3–23.6	22.5		20.2	26.6
Capuchin monkey		24.5	24.6		19.3	17.6–19.2	15.1–17.5
Howler monkey	30.7–34.3	28.3–29.2	26.5–26.7	25 3–26.5	21.3–23.3	20.4–22.6	19.3–21.1
Lemur				48.3		46.4	44.8

Relative width between the eyes

That the eyes of all primates move relatively closer together with advance in growth is shown by the decrease in the relative interocular breadth, as given in table 24. In embryonic life the relative width between the inner angles of the eyeclefts is still at least as great as in adults of most other groups of mammals. The interocular width amounts to more than half the face breadth in human fetuses of the 9th week, but in adult whites to less than one fourth (see fig. 17). The final

degree in this ontogenetic approximation of the eyes reaches different extremes in different primates. The prosimiae contain forms in which the eyes are widely separated (e.g., in the genera *Daubentonia*, *Mixocebus*, *Lemur*, *Propithecus*, and *Indris*), but other forms have very narrow interorbital regions, particularly the genera *Tarsius* and *Loris*. Among the monkeys and apes the eyes have moved relatively closest together in some Capuchin and Guenon monkeys, in macaques and some baboons, and particularly in orang-utan. Adult man has a larger relative interocular breadth than the above named primates. In dolichocephalic whites this proportion seems to decrease ontogenetically to the smallest human values, while in Tasmanians and Hottentotts it is altered least, the eyes remaining relatively farther apart than in other races of man.

There can be no doubt that in the course of evolution of the primates a migration of the eyes towards each other has taken place, very similar to that occurring in the course of growth. This particular phylogenetic process affected man somewhat less than many of the other primates (see also Schwalbe, 1899).

IX. VARIABILITY

Range of variations

In previous chapters it has been shown that human racial characters develop very early in fetal life. The question now arises, whether the individual characteristics of man also appear early in ontogeny. In other publications the author has demonstrated that such bodily features as the shape of the nose (1920), the relations between upper and lower jaw (1925b), the shape of the hand, and the relative length of the limbs (1926) vary fully as much in fetuses as in adults. That individual peculiarities do not develop during adolescence, as is sometimes assumed, but are already clearly defined even in young fetuses, is also proved by the following examples.

Table 25 lists the relative ranges of variation in the hand index at different growth stages. The extreme individual values of this index differ from each other in fetuses for as much as 36.8 percent of the average value. Generally speaking, the shape of the hand tends to vary with practically the same intensity before birth as in adult life, but it has to be emphasized that the most extreme variations occur among the fetuses. This permits the conclusion that the variations in the relative hand width of adults must be primarily of a congenital and not of an acquired nature. Special functions, as, e.g., long continued manual labor, may exert an influence on this proportion, but merely by superimposing their effect on

TABLE 25

Relative ranges of variation (difference between minimum and maximum in percentage of average) in the hand index (hand breadth in percentage of hand length) of white fetuses and adults

AGE	RELATIVE RANGE	AGE	RELATIVE RANGE
9 weeks	24.5	27 weeks	6.7
10 weeks	31.2	28 weeks	22.6
11 weeks	20.9	29 weeks	2.7
12 weeks	30.3	30 weeks	18.4
13 weeks	29.0	31 weeks	14.7
14 weeks	23.8	32 weeks	12.3
15 weeks	36.8	33 weeks	16.8
16 weeks	24.1	34 weeks	21.4
17 weeks	22.7	35 weeks	8.7
18 weeks	20.6	36 weeks	20.5
19 weeks	23.8	37 weeks	17.7
20 weeks	19.7	38 weeks	23.4
21 weeks	36.2	39 weeks	23.0
22 weeks	23.8	40 weeks	16.1
23 weeks	18.5		
24 weeks	24.8	Average for	
25 weeks	16.3	fetal life....	20.9
26 weeks	16.8		
		Adults	22.3

the natural condition (see also Brezina & Lebzelter, 1924).

Figure 19 illustrates the range of variation in the proportion between the lengths of the upper and lower limbs. The arm of fetuses (14 weeks) amounts to anywhere from 106 to 125 percent of the length of the lower limb; in adults these percentages vary only between 79 and 88. This makes it seem more than likely that persons with whether it is merely determined by isolated extremes, if not pathological cases. Figure 20 demonstrates on the example of the cephalic index that the extreme variations are linked by an uninterrupted series of intermediate stages, which are the more numerous the closer they approach the average. The distribution and frequency of the variations in fetuses is as normal as in adults and

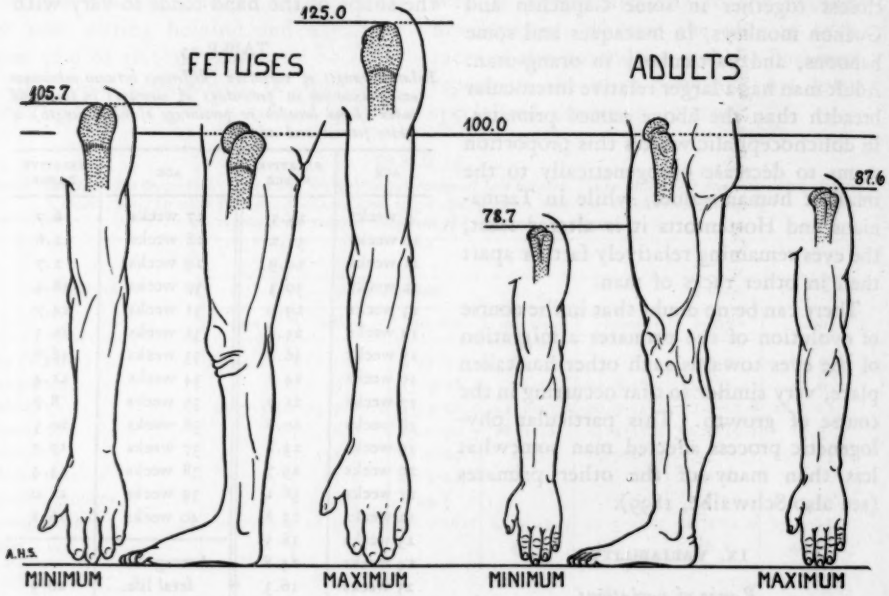

FIG. 19. DIAGRAMMATIC REPRESENTATION OF THE RANGES OF VARIATION IN THE PROPORTION BETWEEN THE TOTAL LIMB LENGTHS OF WHITE FETUSES (14TH WEEK) AND OF WHITE ADULT MEN

Total lower limb length = 100

relatively short arms, as well as those with relatively long ones, must have possessed these distinctions long before they were born and did not develop them gradually in later life.

Distribution of variations

It must be considered whether the range of variations in fetuses is really characteristic for their normal variability, or the extremes, undoubtedly, represent the typical limits of all observed normal variations.

Variability at different ages

Fischel (1896), Mehnert (1896), and others have found a tremendous variability in early embryonic development, indeed, one which is never equalled in later growth stages. According to Minot

(1891), the variability of male guinea-pigs is more than twice as great at the beginning as at the end of postnatal growth. Pearson (1900) showed that man has a much greater variability at birth than in adult life. Woodbury (1921) found a marked decrease in human variability during the first six years of postnatal life. Based upon some of the above quoted data Vernon (1903) had proposed the following law: "The variability of a developing organism diminishes regularly with its growth." Vernon himself called attention to certain exceptions to his "law," and many additional exceptions have been published in more recent years (e.g. Boas & Wissler, 1905).

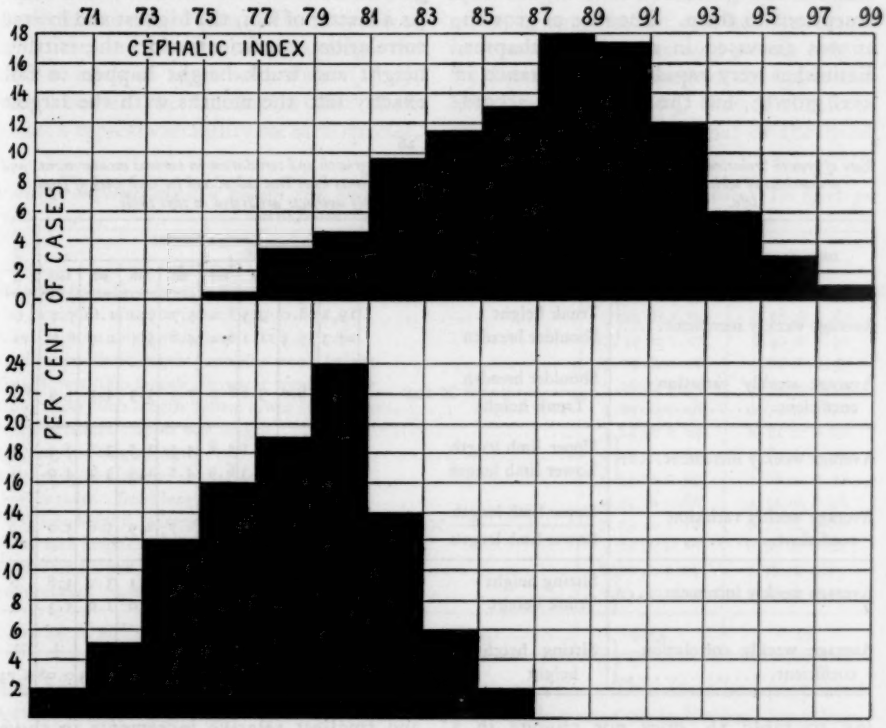

FIG. 20. FREQUENCY POLYGONS FOR THE VARIATIONS IN THE CEPHALIC INDEX (LENGTH : BREADTH PROPORTION OF THE HEAD) OF 200 WHITE FETUSES OF THE THIRD AND FOURTH MONTH (UPPER FIGURE) AND OF 100 WHITE ADULTS (LOWER FIGURE)
Both series from the population of the eastern United States (mostly from Baltimore)

Variability and growth rate

Considerable evidence has been collected for an apparent correlation between variability and rate of growth (Boas, 1896–07; King, 1923; and others), which would imply that the former fluctuates at different ages in accordance with the changes in intensity of the latter. This claim is largely supported by data in regard to postnatal growth. It would seem but consistent to conclude that the

high variability of the embryonic and fetal body is directly due to the rapidity of prenatal growth and that because of this it would be expected that different measurements of the body show little correlation with one another. However, the author's results do not agree with these theories, or, at least, show many exceptions to them. The rate of growth, as was discussed in a previous chapter, diminishes very rapidly with advance in fetal growth, but the variability, according to table 26, does not change in a similar manner. For instance, the largest variation coefficients of the relative shoulder breadth occur in the 5th month, while the measurements, from which this proportion is formed, grow fastest in the 3rd month. The variability in the intermembral index decreases from the 3rd to the 8th months in close connection with the growth rate, but in the 9th month the variability is again nearly as high as in the 3rd month, though the growth rates are 13 to 15 times smaller at the former than at the latter age. The third and last example in table 26 reveals the surprising fact that in certain cases the correlation between two dimensions of the fetal body may even be much closer during periods of rapid growth than when growth has slowed down considerably. As a matter of fact, the highest and lowest correlation coefficients for the sitting height and trunk height happen to fall exactly into the months with the largest and smallest relative increments in these measurements.

TABLE 26

Rate of growth (relative increment per week) and variability and rate of growth and correlation in various measurements and proportions of white fetuses and adults. The increments and coefficients have been calculated for each week of fetal life. For a clear survey of these figures only the monthly averages are listed in this table

INCREMENT OR COEFFICIENT	MEASUREMENT OR PROPORTION	FETAL MONTHS								ADULT
		3rd	4th	5th	6th	7th	8th	9th	10th	
Average weekly increment	Trunk height	29.2	18.0	9.5	8.2	5.7	5.0	1.6	5.4	0
	Shoulder breadth	24.3	19.3	11.1	6.2	4.8	3.5	2.4	6.2	0
Average weekly variation coefficient	$\frac{\text{Shoulder breadth}}{\text{Trunk height}} \times 100$	6.5	8.0	9.6	8.7	7.3	3.3	4.3	5.9	8.1
Average weekly increment	Upper limb length	39.3	23.3	11.1	5.8	4.5	2.5	3.1	4.4	0
	Lower limb length	45.5	24.2	12.3	6.9	4.1	2.9	3.1	4.0	0
Average weekly variation coefficient	$\frac{\text{Upper limb length}}{\text{Lower limb length}} \times 100$	3.9	3.2	3.2	3.0	2.7	1.9	3.6	3.0	2.8
Average weekly increment	Sitting height	26.7	17.6	9.7	6.4	4.9	3.1	3.0	3.8	0
	Trunk height	29.2	18.0	9.5	8.2	5.7	5.0	1.6	5.3	0
Average weekly correlation coefficient	Sitting height and trunk height	+ 0.83	+ 0.71	+ 0.42	+ 0.28	+ 0.24	+ 0.18	− 0.33	+ 0.08	+ 0.73

Variability in different parts of the body

How widely the various body parts and proportions may differ in regard to their variability is demonstrated by the figures in table 27. While a few proportions are more variable in adults than in fetuses, the majority of the proportions show a greater variability before birth than at the completion of growth. However, these

age changes generally do not alter the relative degree of variability in a given proportion. Thus it is found, e.g., that the relation between the upper and the lower limb length has the smallest variation coefficients in both columns of table 27, and that the relative position of the umbilicus is the most variable feature of both fetuses and adults. On account of all these and certain other findings the author tends to agree with Peter (1920), who reached the conclusion that there exists a typical variability for each species,

Compensating variations

Of particular interest in this connection is the fact that the total lengths of the extremities are more constant than their component parts. For instance, the relative range of variation of the total upper limb length (got by adding the lengths of upper arm, forearm, and hand) averages in fetuses of corresponding sitting height 8.5, but the relative range of the upper arm length amounts to 9.9, that of the forearm length to 9.2, and that of the hand

TABLE 27

Variation coefficients and their probable errors for various body proportions of white fetuses and adults. The figures for fetuses represent the averages of 32 weekly coefficients

PROPORTION	FETUSES	ADULTS
Shoulder breadth : anterior trunk height	6.69 ± 0.96	8.06 ± 0.78
Hip breadth : anterior trunk height	7.29 ± 1.09	6.18 ± 0.60
Relative position of umbilicus	13.34 ± 2.07	9.40 ± 0.91
Total upper limb length : anterior trunk height	7.04 ± 1.06	5.82 ± 0.57
Total lower limb length : anterior trunk height	7.18 ± 1.09	5.57 ± 0.54
Total upper limb length : total lower limb length	3.05 ± 0.48	2.75 ± 0.27
Forearm length : upper arm length	4.24 ± 0.64	6.14 ± 0.60
Leg length : thigh length	4.24 ± 0.63	4.60 ± 0.45
Average head diameter : anterior trunk height	6.59 ± 0.99	4.86 ± 0.47
Head breadth : head length	4.45 ± 0.66	4.31 ± 0.42
Total face height : anterior trunk height	7.29 ± 1.10	6.77 ± 0.66
Upper face height : average head circumference	5.74 ± 0.86	6.87 ± 0.62
Upper face height : face breadth	6.70 ± 1.03	7.72 ± 0.75
Nose breadth : nose height	7.77 ± 1.20	7.76 ± 0.75
Average of all (14) proportions	6.54	6.20

each bodily character, and each stage of development. Markedly different variabilities in different species of primates have been described by the author in another paper (1926).

The variability of absolute dimensions on the fetal body can be determined only on specimens of exactly the same age, i.e., size, in order to exclude individual differences due to growth. It suffices to state, that the absolute measurements of fetuses with the same sitting height were found to vary with different intensity in different parts of the body, just as various proportions have different variabilities.

length to 11.2. This must be interpreted as indicating that an individual lengthening of one part of an extremity tends to be compensated for by a relative shortening in another part of the same extremity and *vice versa*. In other words, an acceleration of growth in one segment of a limb must generally be accompanied by retarded growth in another segment. This may be termed "the rule of compensating variations." That this rule is applicable also in regard to adults is apparent from figures, recently published by Todd (1925). This author obtained the following variation coefficients: Total upper limb length

(measured directly) 3.97 ± 0.189; upper arm length 4.93 ± 0.235; forearm length 4.96 ± 0.237; and hand length 4.97 ± 0.237. The variability of the arm segments is so much higher than that of the total arm length that this difference could not be accounted for by the fact that the error in measuring is relatively greater in short than in long dimensions.

The greater variability of the limb segments than of the total limb length explains the fact that the relations in length between corresponding parts of the upper and the lower limb are less constant than

TABLE 28

Relative ranges of variation in white fetuses and adults for the indices expressing the relation in length between the total upper and lower extremity and their corresponding parts

PROPORTION	AVERAGE IN FETUSES	ADULTS
$\frac{\text{Total upper limb length}}{\text{Total lower limb length}} \times 100$	10.35	10.78
$\frac{\text{Upper arm length}}{\text{Thigh length}} \times 100$	15.18	20.71
$\frac{\text{Forearm length}}{\text{Leg length}} \times 100$	16.12	21.17
$\frac{\text{Hand length}}{\text{Foot length}} \times 100$	14.65	12.22

the intermembral index. That this is true for fetuses as well as for adults is clearly shown by the figures in table 28.

Asymmetries

Asymmetries can theoretically be regarded as variations in the two halves of a body. Some brief remarks on fetal asymmetries will therefore be added to this chapter on variability.

The literature contains a number of statements to the effect that asymmetries appear at the earliest during childhood (e.g., Gaupp, 1909). This, however, can not be maintained any longer. Bartelmez and Evans (1926) report that young human embryos exhibit often rather marked asymmetries and the writer (1923) has demonstrated that human fetuses are asymmetrical with great frequency at least after the beginning of the fourth month. Naturally, very precise instruments have to be used in order to detect the asymmetries of small fetuses, and measurements on the skeleton can be taken only immediately after it has been dissected out, so that the cartilaginous parts have had no chance to shrink in drying.

Table 29 compares the frequency and degree of a few asymmetries in fetuses with the corresponding ones in adults. The difference in length between the right and left humerus varies in fetuses from 0 to 7.5 percent of the smaller measurement, the maximum difference in case of the fetal foot length amounts to 7.7 percent, and in case of the ear height to 13.3 percent. These figures show that the degree of asymmetry varies considerably in different individuals and in different parts of the body. In fetuses, as in adults, the humerus is longer on the right side in over half the cases. This early occurrence of a difference in the length of the arms proves that such asymmetries in the adult are rarely, if ever, due to any specialized function, such as right-handedness. Even though the majority of persons use the right arm by preference and may thus give it a greater growth stimulus, one would have to resort to the assumption of the inheritance of an acquired character to explain on that basis the prenatal existence of this asymmetry. The differences in the length of the two feet favor the left side and this in fetuses as well as in adults. For the latter this has also been shown by Matiegka (1893). Asymmetries in the size of the outer ears are very common in man and apparently even somewhat more pronounced in fetal

than in adult life. In ear size there exists no preference, as in the first two measurements, of one side over the other, at least according to the author's findings. In adults Worobjew (1901) found the right ear to be more frequently the larger of the two, but Godin (1910) obtained just the opposite result.

Many more asymmetries exist in other parts of the fetal body, e.g., in the length of the clavicles and in the exact position of the nipples. All these asymmetries are manifestations of a certain independence in the growth of the two halves of one and the same body.

ations are present long before environment could possibly play an important rôle.

A comparison between the variabilities existing in different age groups has one uncertain factor with which to reckon and that is mortality. It is not unthinkable that extreme variations are more likely to die at an early age than variations close to the average. This would tend to reduce the relative range of congenital variations with advance in age. It might be argued, therefore, that the wide range in the variations of some bodily characters of fetuses is subsequently diminished exclusively on account of selective mor-

TABLE 29

Percentage frequencies of symmetry and asymmetries and average differences (including cases of symmetry) between measurements on the two sides (expressed in percentage of smaller measurement) in fetuses and adults

MEASUREMENT	AGE	CASES	Right > left	Right = left	Right < left	AVERAGE PER CENT DIFFERENCE
Humerus length	Fetal	100	52	27	21	1.3
	Adult	105	54	24	22	1.5
Foot length	Fetal	100	33	20	47	1.4
	Adult	500	31	16	53	1.1
Ear height	Fetal	100	39	25	36	2.9
	Adult	100	33	37	30	1.9

Conclusions in regard to variability

It has been shown that not only individuals but even the right and left halves of one body vary no less—indeed, in some cases more—before birth than in adult life. It was demonstrated, furthermore, that at any stage of growth different bodily characteristics have different degrees of variability and that, generally speaking, these typical degrees seem to maintain their relation to each other throughout development. An analysis of these findings leads inevitably to the conclusion that the influence of environmental factors can not be very large and, hence, has often been much overestimated. Variability. Certainly the prenatal death rate eliminates a very large percentage of all variations. From a survey of the literature on this question the author (1921) has reached the conservative conclusion that at most 78 out of every 100 conceptions develop to term. It has to be emphasized that, whereas this explanation is not impossible, it is one which at present can be neither effectively supported nor entirely disproved.

X. SUMMARY

Much could be added to this review of fetal growth, which is far from complete. The data presented were selected particularly from the point of view of the phys-

TABLE 30

The general trend of the growth changes in the more important body proportions of primates, with special reference to man

MEASUREMENT	GENERAL TREND OF RELATIVE CHANGE WITH ADVANCING AGE IN MAN	AVERAGES OF PROPORTION IN WHITES			GENERAL TREND OF RELATIVE CHANGE WITH ADVANCING AGE IN APES AND MONKEYS
		Fetus, 9th week	Newborn	Adult	
Chest circumference	Decreases in relation to trunk height	238	179	170	In principle the same as in man
Hip breadth	Increases in relation to trunk height	42	54	62	In principle the same as in man
Hip breadth	Increases in relation to shoulder breadth	58	84	91	In principle the same as in man
Transverse chest diameter	Increases in relation to sagittal chest diameter	105	119	130	The same as in man, in apes, but opposite in monkeys
Position of umbilicus	Shifts to a relatively higher place on the trunk	16	24	30	The same as in man
Position of nipples	Shifts to a relatively lower place on the trunk except during 6th–10th month of fetal life	80	81	73	Shifts to a relatively higher place on the trunk, i.e., in the opposite direction as in man
Total length of upper limb	Increases in relation to trunk height, except during 6th–10th month of fetal life (decrease)	96	122	145	Principally similar increase and decrease as in man
Total length of upper limb	Decrease in relation to total length of lower limb	133	105	83	The same as in man, though not as pronounced
Total length of lower limb	Increases in relation to trunk height, except during 6th–10th month of fetal life (decrease)	72	116	175	Principally similar increase and decrease as in man, though changes not as pronounced
Forearm length	Increases in relation to upper arm length	72	79	84	The same as in man, though mostly more pronounced
Leg length	Increases in relation to thigh length	65	79	84	The same as in man or no change
Hand breadth	Decreases in relation to hand length	60	53	45	The same as in man
Foot breadth	Decreases in relation to foot length	52	41	37	The same as in man
Thumb length	Decreases in relation to hand length, except during postnatal life	74	68	69	The same as in man
Average head diameter	Decreases in relation to trunk height	95	59	31	The same as in man
Head breadth	Decreases in relation to head length	87	79	77	Mostly no change or sometimes slight change in opposite direction
Total face height	Increases in relation to head height	47	58	85	The same as in man but mostly more marked
Upper face height	Increases in relation to face breadth (decreases slightly before birth)	40	38	56	Generally increases as in postnatal life of man
Nose breadth	Decreases in relation to face breadth	36	24	25	In principle the same as in man
Nose breadth	Decreases in relation to nose height	145	96	62	In principle the same as in man but proceeding more rapidly in most cases
Interocular breadth	Decreases in relation to face breadth	52	25	23	In principle the same as in man

ical anthropologist and in the hope that they may be found useful primarily in the search for the laws governing individual growth and, indirectly, also in connection with the study of the evolutionary specializations in races and species. In spite of the fact that the scope of this paper has been limited, it has been possible to sketch merely the outlines of the many different and often very complicated conditions of fetal growth. To summarize fully this review, which already has had to be condensed to the point of dryness, would entail an undue amount of repetition. This chapter, therefore, is restricted chiefly to the tabulation of the general trend of the growth changes in the most important body proportions (table 30) and to the list of racial differences existing before birth (table 31). These tables illustrate a few generalizations which have not been mentioned above: The majority of the proportions change ontogenetically in a very similar manner in all primates, but the rapidity and the final degree of these changes differ frequently in the various species. The different proportions become altered in the course of growth with widely differing intensity. For instance, in man, according to the averages in table 30, the relative head size changes most (from 95 to 31), the relative length of the lower limb (72 to 175) and the nasal index (145 to 62) change almost as much; however, some other proportions, such as the relative thumb length (74 to 69), are but little different in early and late stages of development. How much the degree of ontogenetic change differs in the various body parts, is also clearly shown by the series of diagrammatic illustrations of the exact body proportions in human fetuses and in an adult (drawn under the author's direction), which have been published in Gray's textbook of human anatomy (21st edition, 1924, fig. 57). All these conditions can be traced to the fact that the rate of growth changes with age and differs in the various parts of the body. This, of course, is not an explana-

TABLE 31

Racial differences between whites and negroes, existing in fetal as well as in adult life. A racial condition marked with is somewhat more "simian" and less "human" than in the other race*

BODILY CHARACTER	IN WHITES (AS COMPARED WITH NEGROES)	IN NEGROES (AS COMPARED WITH WHITES)
Hip breadth in relation to shoulder breadth	Broader	Narrower
Total length of upper limb in relation to trunk height	Slightly shorter	Slightly longer
Total length of upper limb in relation to total length of lower limb	Slightly shorter	Slightly longer*
Forearm length in relation to upper arm length	Shorter	Longer*
Hand breadth in relation to hand length	Broader	Narrower*
Thumb length in relation to hand length	Longer	Shorter*
Finger II longer than finger IV	Not rare	Very rare*
Total length of lower limb in relation to trunk height	Slightly shorter*	Slightly longer
Leg length in relation to thigh length	Shorter	Longer*
Foot breadth in relation to foot length	Slightly broader	Slightly narrower*
Great toe longer than second toe	Frequent	Rare*
Heel prominent	Rare*	Very frequent
Total face height in relation to head height	Lower	Higher*
Nose breadth in relation to face breadth	Much narrower*	Much broader
Nose breadth in relation to nose height	Very much narrower*	Very much broader
Upper lip in relation to upper face height	Lower	Higher
Lips very thick	Never*	Practically always

tion but merely points in the direction in which the ultimate causes are to be sought.

In nine of the bodily characters which show racial differences in fetuses, the whites are more peculiarly human than the negroes; in five other characters, however, this relation is reversed and the negroes are farther removed than the whites from the typically simian conditions (table 31). Incidentally, it should be kept in mind that the term "simian" is not synonymous with "primitive." For instance, the thumb in many respects is more simian in the negro but more primitive or original in the white.

Finally, it has to be mentioned that no racial differences exist in fetuses which are not also present in adults.

XI. GENERAL CONCLUSIONS

In the individual development of different human races or of different primate species, as well as in their evolution, there are theoretically only three kinds of changes possible: The changes may proceed in opposite directions, i.e., their courses may be divergent, or they may occur strictly parallel to each other, or finally, they may converge, thereby reducing the racial or species difference with advance in growth or in evolution. The studies discussed in this paper have not produced a single instance in which the ontogenetic changes converged, either in different human races or in different primates. All human racial differences and all differences between man and apes or monkeys increase during some periods of growth and remain the same during other periods, but they never become less with advancing development. This, undoubtedly, constitutes a strong support for the assumption of a monophyletic origin of the human races and of one common ancestry for all the primates. The much closer resemblance between man, ape, and monkey in early developmental stages than in adult life, can actually not be understood in any other way than by assuming one origin for all from which they inherited the tendency for the same ontogenetic processes, which, in turn, could only have become modified through later specializations. There exists ample evidence for the conclusion that many parts of the human body are less specialized than the corresponding parts of some other primates and hence have remained phylogenetically, as well as ontogenetically, more original and primitive. In a very similar way, it can be stated that the various races of man have become specialized in the different parts of their bodies in widely differing degrees. These relative degrees of evolutionary modification correspond in many instances to the relative extent of the ontogenetic change in the particular structure.

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THE BIOLOGY OF THE TERMITE CASTES

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I. INTRODUCTION

THE question of polymorphism or the evolution of the castes of the social insects such as bees, ants and termites or "white ants" has ever been a troublesome stumbling block to the exponents of the various theories of the evolution of species. Charles Darwin frankly admits in his "Origin of Species" that the question as to how the characters of the sterile workers and soldiers secure representation in the germ cells of the species cannot be satisfactorily explained by the theory which he advocated. There is no doubt but that if the phylogenetic mode of origin of these castes in termites could be determined, this would have a most important bearing on the theories of evolution.

Several methods of attacking the problem may be presented, such as, (1) by the study of fossil insects from the Eocene, where termites first appeared, up to the present time, the Pleistocene; or (2) by taxonomic and morphological studies of termites and their phylogeny; or (3) by biological breeding experiments to determine the type of progeny developing from the various types of reproductive forms within the species, from interbreeding these, and from hybridization.

In undertaking this important problem, involving fundamental biological laws of broad application the aid of many biologists must be enlisted; the subject is too comprehensive for the present small group of enthusiastic students, who are, however, doing all that it is possible for them to do.

The gross anatomy of the digestive systems of termites containing symbiotic intestinal protozoa (Mastotermitidae, Kalotermitidae and Rhinotermitidae) should be compared with termites normally without such intestinal protozoa (Termitidae). More thorough studies should be made of the remarkable post-adult growth and metabolism of the physogastric queens. But little is known of the glandular (both salivary and exudatory), muscular, reproductive and respiratory systems or of the morphology and operation of the sense organs, and studies of them should yield important data relating to the biology of termites. Additional histological studies, such as those made of the brains, eyes and sex organs in 1916 by the late Dr. C. B. Thompson of Wellesley College, are needed.

In cytology, further studies of the chromosomes, such as made by Dr. Alice Boring of Wellesley College, and of the germ cells are necessary before any positive results can be obtained in the genetics of termites. Cytological studies of the eggs in connection with experimentation are needed in all social insects with caste systems. Studies in embryology and physiology are necessary, as well as of the special foods leading to post-adult growth or physogastry of the termites and of some of their insect guests or "inquilines."

The genetics of termites and the study of termite breeding offer a field of special

interest and importance since principles of broad application are involved.

Behavior, biology, ecology, and geographical distribution and relationships studied in connection with intestinal protozoa should yield important results. No careful studies have been made of the ontogeny of the castes, as to the exact numbers of ecdyses or molts of the nymph to adult, and the external and internal metabolic changes incident to each instar; nor of the manner of colonization by the different reproductive forms.

Historical surveys of the work that has already been done in this group may be found in several of the papers listed among the references. The late Dr. B. Grassi of Italy was one of the pioneers in the study of both termites and their intestinal protozoa, although the writer cannot agree with many of his conclusions.

II. TERMITES OR WHITE ANTS

Termites live permanently together in more or less fixed, organized communities or large colonies, as do the other "social insects," such as ants, bees and wasps. Soldiers and workers are included in the parent colony, in addition to the sexual adults and young; that is, there is a caste system, with a more or less closely adhered-to division of labor in the termite community; every effort is for the common benefit of all castes.

While grouped with the social insects, termites are systematically classified in a lower or more primitive order; there are also marked differences in the biology of termites from that of the other social insects.

Termites or "white ants" constitute the separate order Isoptera, of which there are four families, containing approximately one hundred and forty-two genera or subgenera and in round numbers about 1,500 known or described species. These insects occur in all the warmer regions of the world, but reach their greatest numbers and the height of their development in the tropics. In the United States 42 species of termites occur, representing 11 genera or subgenera and the three families, Kalotermitidae, Rhinotermitidae and Termitidae.

Termites are insects of great economic importance, since the principal food of some of the castes of all termites is cellulose. In obtaining this cellulose in its varied forms they directly injure and destroy both living vegetation, crops, and buildings as well as material stored therein. Termites are among the few forest insects that are able to live in and on both decayed and living plant tissue. Often material is also indirectly damaged when it lies in the path of termites as they search for food. Termites do millions of dollars worth of damage annually; such losses occur in both the tropics and in the temperate regions of the world.

While not dominant insects like the ants which *over-run* the tropics, termites by their hidden or subterranean activities silently, secretly and ceaselessly work their insidious damage and are able to *under-run* some tropical countries. A recognition of the powers for destruction or aggressiveness of tropical termites may be seen in such specific names as *atrox*, *bellicosus*, *destructor*, *devastans*, *dirus*, *fatale*, *fatalis*, *ferox*, *militaris*, *molestus*, *mordax*, *pugnax*, etc.

It is especially fortunate that many termite species and genera have received good descriptive names, based on characteristics or habits; i.e., "*flavipes*" (yellow legs), "*lucifugus*," (light shunning), "*perarmatus*" (thoroughly armed), etc. "*Kalotermes*" (beautiful termites) is an especially suitable name for a genus rich in beautiful and striking species. "White ants," "wood lice," "comegen," and

"cupim" (America), "weisse Ameisen," and "fourmis blanches" (Europe), and "anay" in the Philippines are some of the vernacular names (see Hagen, 1855).

Unlike beetles and butterflies, termites are not in general beautiful, and when preserved do not make such a gorgeous display and do not attract amateur collectors. Furthermore, unlike the true ants, they are soft-bodied and very fragile when dry, hence pinned specimens are liable to become shrunken and broken. Nevertheless, while these insects do not attract the attention of general collectors, the study of termites as social insects is fascinating. There are many unsolved problems in their biology and ecology that are of great general interest; moreover, studies of termites can be conducted in this country, as well as in the tropics.

FIG. 1. MACROPTEROUS, WINGED, SEXUAL ADULT OF *Reticulitermes virginicus* BANKS (FAMILY RHINOTERMITIDAE) —ONE OF THE SUBTERRANEAN TERMITES OF SOUTHEASTERN UNITED STATES.

III. THE TERMITE CASTES

Termites are among those insects in which the metamorphosis is incomplete; there is a direct development from egg, to nymph to adult; termites are always superficially "ant-like" in form. No long resting or pupal stage occurs as among insects with a complete metamorphosis; however, quiescent molting stages of relatively short duration occur at each ecdysis. Being in the group of the social insects, there are various different forms or castes within the same species.

In addition to the sexual, winged (macropterous), colonizing, reproductive adults (fig. 1), and its deälated form, there are brachypterous and apterous reproductive adults (fig. 2) of both sexes and also a series of "intermediate" forms ranging from macropterous to apterous adults. Sterile as well as sexual forms exist, and are called workers and soldiers (fig. 3); each caste consists of individuals of both sexes, but the workers and soldiers normally possess non-functional sex organs; there may be two different types of workers and three different types of soldiers of the same species of termite.

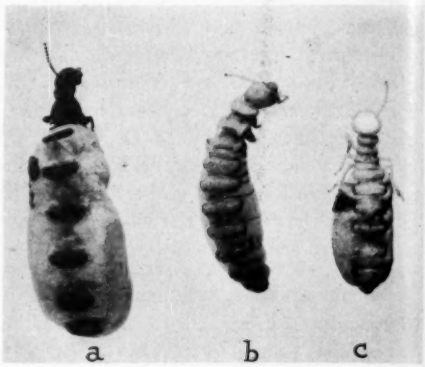

FIG. 2. EGG LAYING, POST ADULT FEMALES OR QUEENS OF THE MOST COMMON, SUBTERRANEAN TERMITE OF EASTERN UNITED STATES, *Reticulitermes flavipes* KOLLAR.

(*a*) Queen with wing stubs (deälated) developed from the macropterous colonizing form; (*b*) brachypterous form; (*c*) apterous form; these queens have corresponding males and the types interbreed in nature.

The evolution and biology of these castes among termites have always been problems of great general interest to biologists. There are two views as to the origin of the castes, both based on observation and experiment. According to the first view, held by Grassi (1893) and later by Jucci (1920 and 1924), the young are all alike and undifferentiated at the time of hatching, but differentiate into the various adult castes through the influence of external factors of the immediate environment such as food, or because of castration by intestinal proto-

zoan parasites, or as a result of the care received from the workers, etc.

Adherents to the second view, are the late Dr. C. B. Thompson of Wellesley College (1917–1922), Dr. T. E. Snyder (1913–1926), the distinguished Swiss entomologist Dr. E. Bugnion, the noted British entomologist Dr. A. D. Imms, as well as many others; they claim that the young are *not* all alike at the time of soldiers from the eggs were erroneous, but other data presented by him confirm the ontogenetic origin of the termite castes.

It is believed by the writer that the histological studies conducted by Miss Thompson have proved that the ontogenetic origin of the termite castes is due to *intrinsic* causes of germinal origin and *not* to *extrinsic* stimuli which for many years have been credited with formative—

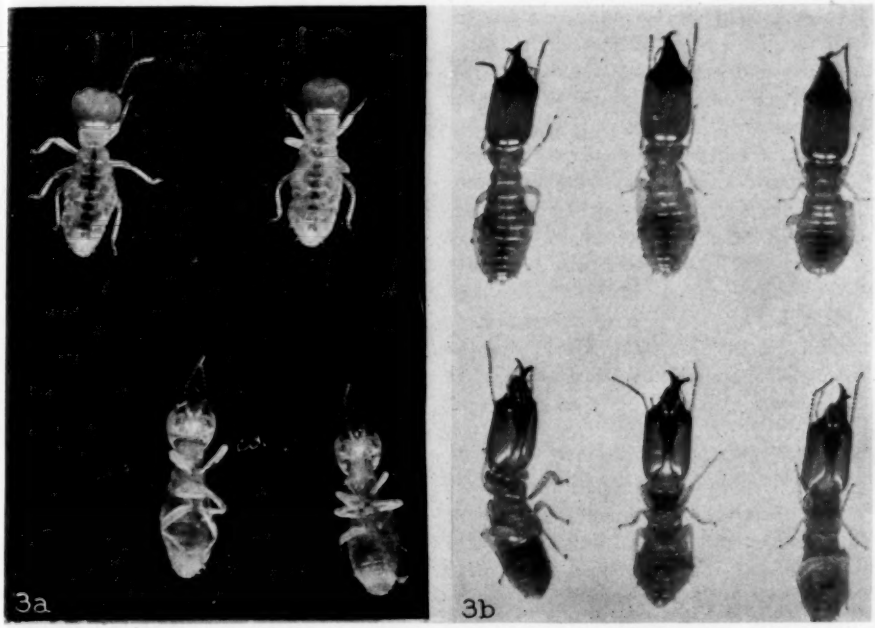

FIG. 3. (*a*) WORKERS AND (*b*) SOLDIERS OF *Reticulitermes flavipes* KOLLAR; THE COMMON SUBTERRANEAN TERMITE OF THE FAMILY RHINOTERMITIDAE OF EASTERN UNITED STATES

hatching, but the castes are hereditary. Some, if not all, of the different castes are distinguishable from the beginning and the castes are therefore predetermined in the egg or embryo by intrinsic factors.

Bugnion (1913–1920) was the first modern biologist to present evidence that the castes of termites are determined in the egg. His observations on the hatching of externally, maturely developed indeed almost creative—powers. Which of these views is correct? Or are they both in part true?

The fertile and sterile types even as nymphs are internally differentiated at the time of hatching, and very early in their postembryonic development all of the adult castes may be distinguished. These facts disprove the older hypothesis that castes may be determined or changed

by external means. A natural explanation is that the castes have originated by segregation from a heterozygous parent form. Preliminary studies by Boring reveal no visible differences in the chromosomes of the various castes.

In collecting termites for study, every effort has been made to obtain as many of the forms or castes as possible; specific descriptions and identifications are based either on the winged or soldier caste, and it is essential to obtain winged adults or soldiers. However, some specific as well as family and generic characters occur in the worker caste in certain genera; the worker caste should receive further study. Species in most genera in the family Kalotermitidae have no worker caste, the duties of the workers being performed by the young or nymphs, whereas in the genus *Anoplotermes* Fritz Müller in the family Termitidae, the soldier caste is lacking. It is necessary to collect the winged forms or the queens in order to make specific identifications in the genus *Anoplotermes*.

IV. THE TAXONOMY OR CLASSIFICATION OF TERMITES

The most complete and satisfactory classification of termites, based on world collections, is that of the distinguished Swedish entomologist Holmgren (1909–1913); this most nearly approaches a natural system. While this classification is accepted in general by American workers in this group, certain minor phases are rejected, and others are temporarily accepted with reservation, as for instance, the validity of certain subgenera, especially of *Kalotermes* and *Nasutitermes*.

According to Holmgren, there are in the order Isoptera four families, ranging in degrees of specialization from the Mastotermitidae and Kalotermitidae through the Rhinotermitidae to the most highly specialized family the Termitidae.

Winged adults of the living species of the Mastotermitidae (there being one living and four fossil species) have large anal and postanal fields in the hind wings, the humeral suture or point of breakage is absent in the hind wing, the fore-wing scale is large; there are 5 tarsal joints; the fontanelle is absent; ocelli are present; the pulvillus between the apical claws on the tarsi of the legs is present; the pronotum is flat. Both soldiers and workers are present. Macropterous and apterous reproductive forms occur in colonies.

In the winged adults of the species of the Kalotermitidae, the postanal field and enlarged anal fields are lacking in the hind wing, but in this wing there are sometimes rudimentary anal branches, the humeral suture is incomplete (as in *Termopsis*) or complete, the fore-wing scale is large (small in *Hodotermes*), the wings are usually reticulated; 5 to 4 tarsal joints; fontanelle absent; ocelli present (or absent in *Archotermopsis*, *Termopsis*, *Hodotermes* and *Porotermes*—"false ocelli" occur in *Hodotermes*); pulvillus *usually* present (normally absent in *Hodotermes* and *Porotermes*). Soldiers are present, but workers are absent, except in *Hodotermes*. Macropterous, brachypterous, and apterous reproductive forms occur, the prevalence of a certain type varying with the genus.

Holmgren has established the four subfamilies Termopsinae (*Archotermopsis*, *Hodotermopsis* and *Termopsis*), Hodotermitinae (*Hodotermes*, *Macrohodotermes* and *Anacanthotermes*), Stolotermitinae (*Stolotermes*), and Kalotermitinae (*Porotermes* and *Kalotermes* l.s.).

The genus *Termopsis* in the subfamily Termopsinae is more primitive than the genus *Kalotermes* of the family Kalotermitidae, because the contained species are not so well defined in *Termopsis* as in *Kalotermes* of the subfamily Kalotermitinae. In the latter genus, some species are very distinct and the species are more numerous than in

Termopsis. In species of *Kalotermes* there is a reduction in the number of antennal segments. However, ocelli are present in *Kalotermes* but absent in *Archotermopsis*, *Termopsis* and *Porotermes*. The presence of ocelli is a primitive character. Workers are absent in *Archotermopsis* and *Termopsis*.

In the subfamily Hodotermitinae, species in the genus *Hodotermes* (l.s.) are grass or leaf-cutting termites and in their structure and pigmentation, they also show considerable progressive development; ocelli are absent but "false ocelli" are present. While they nest in *subterranean* cavities and galleries, they are termed "wander-termites," since both the workers and soldiers of some of the species are darkly pigmented, have faceted eyes and long legs, and forage above the ground during the day exposed to the sunlight, as do some of the more highly specialized Termitidae. In the subgenus *Macrohodotermes*, soldiers are never (or seldom) seen outside of their burrows during the day. In *Hodotermes* (l.s.) the pronotum is sellate or saddle-shaped—a specialized progressive character. There are no secondary sexual characters to be seen in the apex of the abdomen; both sexes possess styli. In *Macrohodotermes*, however, abdominal styli are atrophied or missing, indicating a progressive reduction.

The presence of this highly specialized worker caste gives some credence to the view that *Hodotermes* might be classified in a distinct family the Hodotermitidae, possibly related to the intermediate Rhinotermitidae; ocelli are sometimes lacking in species of *Leucotermes* in the latter family. Furthermore, in the genus *Serritermes* in the Rhinotermitidae, there is also a highly specialized worker caste and these termites are foraging in habit. Preliminary studies of intestinal protozoa by Dr. Harold Kirby, Jr., of Yale University rather indicate such a relationship between *Hodotermes* and the Rhinotermitidae. However, all phases of the subject should be much more thoroughly studied before any such radical change could be accepted.

In the primitive genus *Kalotermes* of the subfamily Kalotermitinae, now classified as closely related to the genera *Termopsis* and *Hodotermes*, ocelli are present—a primitive character; there is also color in the reduced eyes in the soldier in some species. Hagen in 1858 considered *Kalotermes* to be the most primitive genus known. The pronotum is arched and of the blattid type (Fuller, 1924). No worker occurs in any of the species in this subfamily.

In *Porotermes*, however, in the same subfamily with *Kalotermes*, ocelli are absent. *Porotermes* was formerly considered to be a subgenus of *Hodotermes*, since the subcostal vein in the wing is absent or rudimentary. According to Kirby, the intestinal protozoa of *Porotermes* appear to be related to those of *Hodotermes* and the Rhinotermitidae as well as to the flagellates of *Kalotermes*.

In the intermediate family Rhinotermitidae, the fontanelle, with few exceptions, is present in glandular form; the fore-wing scale is large (except in *Psammotermes*), the wings are usually reticulate, the reticulation of the wing membrane becomes rudimentary and almost disappears in the higher subfamilies; the pulvillus is absent. The pronotum is subcordate to slightly saddle-shaped. In *Serritermes* both the soldiers and workers are highly specialized as "wander" termites. Macropterous, brachypterous and apterous reproductive adults occur in colonies; both of the latter forms are common, but brachypterous adults have become the more highly specialized.

Six subfamilies of the family Rhinotermitidae have been established by Holmgren.

The most highly specialized termites are in the family Termitidae; the fontanelle always has a plate-like structure; the forewing scale is small; the wings are not strongly reticulate; the pulvillus is absent. Workers and soldier are present, except in *Anoplotermes* where the soldier is lacking. The pronotum is sellate, and specialized thoracic spines occur on both the soldiers and workers of certain "wander" termites (*Syntermes* and *Acanthotermes*). Macropterous and brachypterous reproductive adults occur, but the apterous form is apparently lacking or, if it occurs, is very rare; its disappearance is a progressive development from the lower termites.

Holmgren has established four subfamilies in the family Termitidae. The Termitinae (including the *Termes* or fungus-growing group); the *Syntermes* group, which includes foraging and harvesting termites (in *Syntermes* and *Speculitermes*); *Amitermes* (including the Australian termite with "compass" mound nests); and the *Miro-Capritermes* group; in the latter group are those termites whose soldiers have asymmetrical, non-biting mandibles. The Microcerotermitinae, Pseudomicrotermitinae and Foraminitermitinae are the other subfamilies.

V. THE PHYLOGENY OF TERMITES AS EVIDENCED BY PALEONTOLOGY, TAXONOMY AND BIOLOGY

Although termites have a close systematic relationship with the roaches or Blattidae, they are much younger geologically, and therefore more recently evolved. No fossil termites are known from the Mesozoic Age, but termites may have existed in the Cretaceous period; they occur in all deposits from the Lower Tertiary on.

As Holmgren concludes, both termites and roaches are probably offshoots of a more primitive group. None of the fossil termites are more generalized or more primitive than living termites. Indeed, a living species of the genus *Mastotermes* Froggatt of Australia is the most primitive (Froggatt, 1895–1923); this termite has a wing structure similar to the roaches, remarkably developed reproductive organs in the female, and recently (1925) Hill has discovered that the egg mass is similar to the oötheca of the roaches indicating at least common ancestry. However, three species described as *Mastotermes* by Von Rosen (1913) have also been found as fossils in the Tertiaries of Great Britain and one in Croatia. Nevertheless, in prehistoric times there was naturally a greater prevalence of primitive termites than at present.

The wings of the large and most primitive living termite, *Mastotermes darwiniensis* Froggatt in the family Mastotermitidae, the lowest termites, have a large anal field, as in roaches. This most primitive termite (in the *lowest* family) has a soldier much more specialized than would be expected; this soldier and the worker of the same species were erroneously described by Froggatt, after he had already described the winged adult, as *Termes errabundus* and placed in the family Termitidae, which contains the *highest* termites. Even in this primitive species the worker caste is present, although this caste is usually lacking in the next higher family, the Kalotermitidae.

According to Caudell (Snyder, 1924), in the wings of certain roaches a break often occurs following in general the anal sulcus at the base resembling the humeral suture of termites, where the wing breaks off after flight; in primitive termites this suture is also often poorly defined. In the biology of termites and roaches there are other similarities based on homologous structures, but termites have become more highly specialized and have become social

in habit, with a well-developed caste system. Even the most primitive termite *Mastotermes darwiniensis* is a very destructive wood borer, with diffused nests containing large numbers of individuals.

Roaches seldom are found boring in *sound* wood; the logs that they inhabit are usually decayed, and they utilize the burrows of wood-boring insects, or live under the logs, or between the bark and wood. However, a large, brown, wingless roach (*Cryptocercus punctulatus* Scudder) lives by burrowing in *fairly solid* wood in partly decayed chestnut and coniferous (pine and fir) logs in the Appalachian Mountain region and on the Pacific Coast.

According to Kirby, domesticated roaches contain the only Hypermastigate flagellate not found in termites, a flagellate related to those of some of the Kalotermitinae. It would be extremely interesting to study the protozoa of the roach *Cryptocercus* from its native habitat, since this insect apparently eats the wood through which it burrows. The wood may be so decayed, however as to be broken down already by wood-destroying fungi.

Some of the primitive termites (*Archotermopsis* and *Termopsis*) normally inhabit the wood of conifers but not that of Angiosperms, which are geologically more recent plants. This, however, may be due to the fact that the common habitat of these termites and conifers is in a colder climate than is usual for most termites, although these termites are among the oldest (geologically) that have been found as fossils.

The young or nymphs of certain species of *Kalotermes*, *Prorhinotermes* and *Coptotermes*, possess wing pads on the pronotum; these later disappear in the development of the nymph to the adult. The appearance of transitory, vestigial wings so early in the ontogeny of termites is another indication of the recapitulation of the phylogeny of termites, since (Imms, 1919 and Fuller, 1924) similar alar structures also appear on fossil orthopterous insects (Carboniferous). Both the Isoptera and Orthoptera were derived from a common ancestor.

Species of *Zorotypus* of the southern United States in the order Zoraptera Silvestri are gregarious and have *both apterous* and *winged* reproductive forms as in the most primitive termite (*Mastotermes*); the latter forms lose their wings after flight in a manner similar to that in the lower termites, the point of breakage being poorly defined; there is also a tendency to variation in wing venation among individuals as in termites; the reproductive organs are well-developed. No worker or soldier castes exist in *Zorotypus*, but it is believed by the writer that these insects are closely related to termites and that *Zorotypus* is at the dawn of social life. The habitats of these insects are in situations similar to those where termites live and they superficially resemble young termites, but move much more rapidly. It is not known whether intestinal protozoa occur in species of *Zorotypus*.

As Crampton has shown (1920), in *Mastotermes* there is a remarkable development in the alate female of a fully formed ovipositor. The external genitalia are unlike those of any other termites (where they are reduced) resembling in general the arrangement in the roaches. This is an indication that the primitive termite *Mastotermes* is most nearly related to ancestors non-social in habit.

VI. THE PHYLOGENY OF THE TERMITE CASTES AS EVIDENCED IN THEIR ONTOGENY

While there are no authentic paleontological records of termites before the Tertiary, Wheeler has stated (1923) that

"in all probability the termites, like the ants, reached their complete structural and social development in the late Cretaceous or early Tertiary and have since undergone very little modification."

It is believed that the ancestral termite, like the ancestral roach, consisted of merely winged males and females. The only fossil forms of the most primitive termites found have been winged. The prototype of both termites and roaches was also probably winged, although insects originated from a worm-like ancestor.

The records written by fossil termites are at best very imperfect. While it has not been proved that wingless termite castes occurred in the Tertiary period, they doubtless occurred and were probably evolved during the late Cretaceous period. Polymorphism among the social insects may not have been as highly developed as at present, especially in the case of the reproductive forms, but it can not be stated that the sterile castes and colony or social habits developed since Tertiary times because of lack of fossil forms. Due to their habits, such sterile forms would be less likely to be preserved as fossils. Both mandibulate soldiers and nasuti in clearly differentiated fossil form have been found embedded in gum copal from the Pleistocene period of comparatively recent formation.

It does not seem probable that the elaborate polymorphism that occurs today existed among the reproductive castes in termites during the Tertiary period; it is believed that a greater polymorphism probably has come about since the Tertiary.

At least two other dissimilar or distinct, sexual, colonizing adults, as well as a series of intermediate forms have evolved from the original macropterous or winged form. Both brachypterous and apterous reproductive adults occur in some of the most primitive or lowest living termites. Apterous forms are common in *Mastotermes*, *Termopsis*, *Hodotermes*, and more rare in *Kalotermes*, as well as common in the next higher termites, the Rhinotermitidae; however, brachypterous reproductive adults do not occur in *Mastotermes*.

Fuller of South Africa has sent to the writer specimens of a yellowish, apterous caste, larger than the worker that is found with species of *Macrohodotermes* Fuller; this caste has black pigmented eyes and may be a third form (apterous) reproductive adult. Also an apterous queen of *Hodotermes* (*Anacanthotermes*) *ahngerianus* Jacobs. of Turkestan is figured by Vasiljev (Revue Russe d' Entomologie XI, 1911, pp. 235–245); the color of the head of this apterous form is brown and the eyes are black-brown.

Brachypterous reproductive forms while absent in *Mastotermes* are common in *Termopsis*, but are rare in *Kalotermes*, again becoming common in many of the Rhinotermitidae.

Among the highest termites (Termitidae), while brachypterous adults commonly occur (in *Armitermes*, *Nasutitermes* and *Microcerotermès*), apterous forms are apparently lacking.

These three reproductive adults develop from nymphal prototypes similar to the adult (unlike in the case of the soldier caste). Presumably, a direct development is also the case in the "intermediate" reproductive forms.

While both the worker and soldier castes occur in the most primitive termites (*Mastotermes* and *Hodotermes*), the worker is absent in other primitive groups (*Archotermopsis*, *Termopsis*, *Kalotermes* and *Porotermes*) but occurs in all the intermediate and in the highest termites. Hence, there is some doubt as to the evolution of the worker and soldier castes and as to which was derived first.

Fuller believes that the very highly specialized worker caste present in *Hodotermes* has been lost in *Termopsis* and *Kalotermes* as the soldier has been lost in *Anoplotermes*, one of the higher termites.

Soldiers of primitive termites are of only one type (are monomorphic); in the intermediate termites they become impressively dimorphic; and in the higher termites trimorphic; but among the most specialized termites they again become monomorphic.

Among some of the species of *Termopsis* and *Kalotermes*, a small proportion of the soldiers in the colonies are commonly found to have wing pads or vestigial wings. Indeed, in a very primitive and the largest known species of *Kalotermes*, namely, *K. occidentis*, described in 1853 from the soldier caste by Walker from the West Coast of Central America, and also occurring in Arizona and Lower California, every specimen of soldier which has been found in the colonies has vestiges of wings or rudimentary wing pads. It is believed that this is a primitive or ancestral character; or a reversion to the condition when all the present "social insects" were merely male and female winged forms with no sterile worker or soldier castes.

Holmgren established a new subgenus (*Pterotermes*) for this termite (*occidentis*), which is merely a primitive *Kalotermes*. The reduced eye spots of the soldier have a black color, as is the case in several other species of *Kalotermes;* the eyes are not, however, to be compared with the well developed pigmented eyes of the soldier of *Hodotermes*. Winged adults of *K. occidentis* recently have been found and described by Banks (1920).

No workers with wing pads ever have been found among any of the termites. Furthermore, in some primitive termites (*Archotermopsis* and *Termopsis*) there are indications that female soldiers are fertile and able to lay eggs, a reversion to the ancestral state when only male and female adults were present. In these two genera there are also external secondary sex characters in the soldier caste. Although there is an "ergatoid" or worker-like, apterous reproductive form in termite colonies, no potential or egg-laying workers ever have been found.

Does the ontogeny of the soldier caste, which develops from a very different, worker-like prototype, recapitulate the phylogeny of the soldier caste, or did the worker caste evolve from the soldier? This latter view of the derivation of the worker caste was first advocated as a theory by Emerson of the University of Pittsburgh, and was based on studies of the ontogeny of the soldier in a *Constrictotermes*.

Genetic formulae for termites would show that the broods differ not only with the age of the colony but also with the genus and species. Of the first brood in young colonies of species of *Reticulitermes* (of the intermediate family Rhinotermitidae) in the United States (a genus where both soldiers and workers occur) most are workers and a few soldiers, but *there are no sexual forms*. This is exactly the reverse of what is believed to be the phylogeny of the termite castes. The first brood of the species of *Termopsis* of the lower family Kalotermitidae consists of nymphs of the sexual forms and of soldiers—a more proper representation of the phylogeny of the castes.

A comparison may be made of the phylogeny of the fertile and sterile termite castes, as evidenced in their ontogeny, with the phylogeny of the fertile and sterile portions of a plant. In the white, sweet-scented water lily (formerly *Castalia*) now *Nymphaea odorata*, some of the anthers have been transformed into petals; all gradations between anther and petal

may be seen in a single flower. These petals may be less important functionally than the anthers, yet each serves a purpose. The sterile soldier termites—more highly specialized than the workers—are less important functionally than the workers and both are less necessary than the fertile forms from which they have developed. They all serve needs in the colony life.

This relative ratio between the numbers of soldiers and workers in colonies of termites holds during the second year, when sexual adults are also produced in colonies of *Reticulitermes*. In old colonies, workers (in genera where present) always greatly out-number the soldiers among *all* termites, which constitute but a small proportion of the castes in the nest; large numbers of sexual adults develop to maturity each year.

Workers are much more useful and independent than are the soldiers which need to be fed by the workers and whose effectiveness in protecting the colony in some species and genera is doubtfully as great as that of the workers. In one over-specialized genus (*Anoplotermes*) among the higher termites, the soldier caste is lacking. In this genus the workers are—both as to legs and mandibles—specially modified.

Soldiers may occur in as many as three different types (are trimorphic) in some of the higher termites and are dimorphic in some of the intermediately classified termites; whereas, the workers at the most occur in only two types in the higher termites. These facts indicate a greater specialization of the soldier caste, and possibly that this caste evolved before the worker.

Winged termites in the course of their specialization have developed the complete humeral suture and have lost the strong power of flight of the lower forms; the reticulation of the wing membrane disappears; the wings are reduced so that in the Termitidae only about the middle portion remains; and the anterior wing scale becomes markedly reduced in size. There is the usual reduction or loss of veins in the wings from the lower to simpler-veined, higher termites; the costal area is markedly reduced. The pronotum develops from a flat type to the sellate form. The shape and position of the head with relation to the pronotum changes, the progression being to a condition of reduced mobility. Abdominal cerci and styli (atrophied or missing in *Macrohodotermes*), tarsi, lateral tibial spines and the pulvillus of the legs become reduced or lost in regressive development; although long antennae and legs again appear in the "wander" termites among the Termitidae.

The reproductive forms become polymorphic from the lower to higher termites and from relatively small, active, and less dependent forms they develop to very large, inactive forms, entirely dependent (on the workers) in the higher termites. The presence of dependent queens occurs only among termites with workers present. Why do not the nymphs take the place of the workers in this rôle?

This development of the queens is correlated with progressive evolution in the building of more permanent specialized nests. Among the lower termites the more or less temporary nests are nearly always diffused, whereas in the higher, nests are more permanent, concentrated and specialized, in *Apicotermes* of the Belgian Congo reaching a utilitarian and architectural development not exceeded even by the higher insects (the Hymenoptera).

In all of the lower and intermediately classified termites, intestinal protozoa which aid in the digestion of wood are

present. But in the highest termites (the Termitidae) protozoa are few and of the type found parasitic or commensal in other insects. So far as is known they do not play a symbiotic, helpful rôle.

The common apterous reproductive form in the lowly Mastotermitidae and Kalotermitidae and intermediate Rhinotermitidae, first becomes supplemented in the Kalotermitidae by brachypterous reproductive forms, and finally the apterous form disappears in the higher Termitidae.

In some species in the intermediate family Rhinotermitidae and higher Termitidae (in *Armitermes*), the winged or macropterous forms do not appear to be the dominant reproductive type, as is usual among the lower termites. This is especially true in species of the non-subterranean, island genus *Prorhinotermes* where apterous reproductive adults are most commonly found heading colonies in moist wood in wet sites; brachypterous reproductive adults do *not* occur in colonies. It is believed that these termites (*Prorhinotermes*) are largely dispersed in drift wood—and that colonization is by division of colonies as well as by flight.

In the species *P. simplex* Hagen in Florida no nymphs with long wing pads have ever been found in colonies although these forms occur in colonies of this species in Cuba.

In *Prorhinotermes molinoi* Snyder of Central America, the winged adult appears to develop from a nymph with short, circular, apparently fused wing pads. So far as can be seen from a series of specimens in alcohol from Costa Rica, these wing pads become markedly inflated just before the penultimate molt; they become raised up apically from their normal flat position and a median suture appears. This is a marked departure from the normal condition in other termites where the winged adult develops from a nymph with long, straight wing pads.

Also, in the progress from the lower to the higher termites, the functional (as biting) mandibles and rudimentary frontal gland of the soldier caste show marked changes (fig. 4). In the intermediate family Rhinotermitidae, the frontal gland is a highly specialized organ of defense—a sticky white secretion exudes from a short tube—which is very effective against insect enemies; the labrum is also highly specialized (fig. 5); but the mandibles are functional. The pronotum changes from the ancestral flat shape to a somewhat

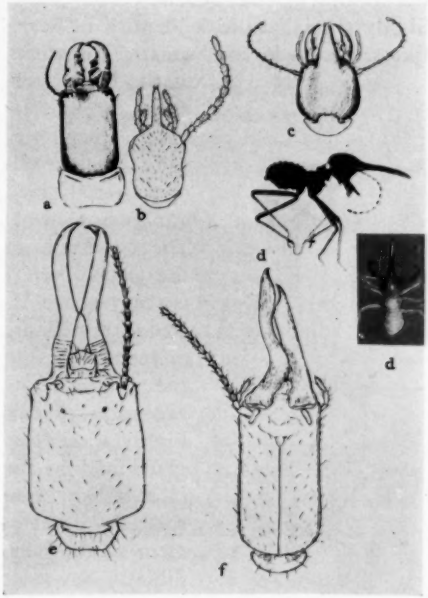

FIG. 4. VIEWS OF THE HEADS AND PRONOTA OF SOLDIER TERMITES TO SHOW REGRESSIVE DEVELOPMENT IN THE DEVELOPMENT OF THE MANDIBLES AND PROGRESSIVE DEVELOPMENT OF THE FRONTAL GLAND, FROM THE KALOTERMITIDAE (*Kalotermes*, (*a*)) TO THE TERMITIDAE (*Nasutitermes*, (*b*)).

In the family Termitidae is also seen a transitional genus (*Armitermes* (*c* and *d*)), where both mandibles and frontal gland are functional; also in this family, there is an overspecialization in the mandibles (*Orthognathotermes* (*e*) and *Neocapritermes* (*f*)).

saddle-shaped structure,—a progressive development—; and there is progressive development in the clypeus and postclypeus; the latter becomes markedly arched and bilobed in the higher termites.

While, in many of the higher termites, the mandibles are absent or vestigial and the frontal gland becomes even more highly specialized as a "nasus" or beaklike structure in the "nasuti," in others of the higher termites (*Armitermes*) both mandibles and well-developed frontal gland are functional. The condition in the genus *Armitermes* may be considered as transitional or intermediate in the progress of the evolution of this highly specialized gland and in the later reduction or regressive development of the mandibles. In some species of *Armitermes* the mandibles are more dominant than the frontal gland, in others the reverse is the case. In *Acanthotermes* the outlet of the frontal gland is remarkably modified.

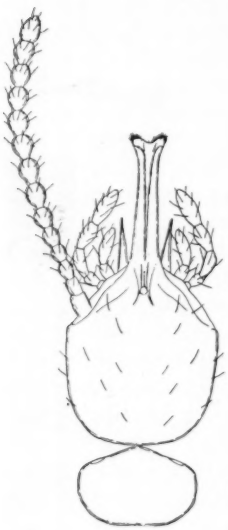

FIG. 5. HEAD AND PRONOTUM OF THE MINOR SOLDIER OF *Rhinotermes latilabrum* SNYDER TO SHOW HIGHLY SPECIALIZED LABRUM AND FRONTAL GLAND, AS WELL AS VESTIGIAL MANDIBLES.

According to Holmgren (1912), in *Termes horni* and *T. ceylonicus* Wasmann the salivary glands are developed as defense glands.

In *Anoplotermes*, a genus of the higher, over-specialized termites, the soldier caste is lacking but the workers and winged adults often have very long mandibles. Or in other over-specialized forms, the mandibles of the soldier become extended, lose the marginal teeth and do not function for biting, but are twisted and asymmetrical and are used in flipping themselves away from danger or flipping particles of dirt at invading insect enemies. The labrum also becomes progressively developed.

Morphological evolution in the soldiers of the over-specialized fungus-growing *Termes* series is generally regressive in character as is the caste system; this regression is correlated with regressive development of the nest structure. The entire system of life economy of the nest among these fungus-growing termites, which are confined to Ethiopia and Indomalaya, is most highly specialized, as evidenced by the mound nest, the huge queen imprisoned in a protected "royal cell," "nurseries" and "fungus gardens" —a sponge-like mass where special fungi are grown for food (the conidia are cropped as food by the young and are also fed to the reproductive adults). Dependence is not placed entirely upon the cellulose of wood, which has to be broken down by intestinal flagellates. Such protozoa which aid in the digestion of wood are absent in tne intestines of species in the *Termes* group.

The Indian species *Hospitalitermes monoceros* Koenig has workers deeply-pigmented, with eyes well-developed and long legs, which forage above ground in the sunlight; they harvest portions of lichens for food.

Also, in the worker caste there is a progressive loss or reduction in the number of marginal teeth on the mandible, from the lower to the higher termites, and a progressive development of the frontal gland. A marked progressive development in the workers of the higher termites is the structure and marked color of the

diurnal harvesting or "wander" termites —grass or leaf-cutting species. The heads are larger than usual, the legs and antennae are often very long; the antennae have more segments than related non-wandering species—primitive characters. The intestines and salivary glands show progressive development. Among these termites are: *Hodotermes* (l.s.)—Palearctic, Ethiopian and Oriental; *Serritermes*—Neotropical; *Termes* (l.s.)—Ethiopian and Oriental; *Syntermes*—Neotropical; *Acanthotermes*—Ethiopian; *Nasutitermes* (l.s.) Neotropical and Oriental; *Speculitermes*—Neotropical and Oriental; *Drepanotermes*—Australian; all except *Hodotermes* and *Serritermes* are in the family Termitidae and lack symbiotic intestinal protozoa.

The fact that the termites of the primitive genus *Hodotermes* have a highly specialized worker caste and that they are diurnal foraging and harvesting termites—as are some of the higher termites—is difficult to explain on the basis of progressive or regressive development under the present classification of *Hodotermes*. However, in *Hodotermes* there are many primitive characters evidenced in antennae, wings, tarsi, tibial spines and cerci and in the presence of intestinal protozoa; there is no reduction to indicate progressive development. Nevertheless, in the "wander" termites among the Termitidae, there is a similar lack of reduction in antennae and legs—a regression.

VII. THE BIOLOGY OF THE TERMITE CASTES (GENERALIZED)

The "first-form" or macropterous queen produces five to seven kinds of offspring (varying with the species), one to three fertile and two to five sterile types—only one type being like itself (the parent), the others all different in structure and behavior.

There is a parallelism between termites and Mendelian "segregants," where there is a splitting up of a complex parental hereditary material into many simpler types of offspring or segregants. Various less common, abnormal or "intermediate" reproductive adults of termites are merely other segregants.

Since we believe that it has been proved that the fertile and sterile castes are differentiated at the time of hatching and since there is no positive proof that special qualitative feeding can determine the castes (and indeed there is much evidence to disprove this) and that intestinal protozoa do not cause sterility in the neuters, but have a symbiotic relationship, the explanation of the origin of the castes due to immediate environment, such as food, can not be accepted. The castes in termites are undoubtedly blastogenic in origin. To regard them as segregants appears to be the most inclusive and plausible explanation.

At certain seasons (spring or autumn) of each year, winged, sexual, colonizing forms of both sexes appear in large numbers, in well-established colonies. Normally termites shun the light, but these forms, impelled by some irresistible impulse to leave the colony, temporarily become markedly positively phototropic. After the short, "wobbly" flight or "swarm," the deälated adults become strongly thigmotropic; they must have contact with wood or earth.

The lower termites have a longer, stronger flight and emerge from the parent colony in smaller numbers and at irregular intervals, while the more specialized termites are restricted to a few large flights annually; the humeral suture is well defined in the higher termites (Termitidae), which sometimes lose one or both pairs of wings in mid air, and then spiral to earth. The lower termites, however, are forced to pry off their wings, since the humeral

suture or line of weakness is but poorly defined.

In general, the stimuli in the termite colony are hunger, sex and fear, and in the progressive development of termites, greater specialization can be observed in food, reproduction and defense. Nevertheless, the synchronous swarming of the winged, sexual, colonizing adults is one of the rhythmic activities in the life of the termite colony which is but little understood. At a certain time on the same day thousands of winged adults will emerge from different colonies of the same species of *Reticulitermes* in logs, stumps or infested buildings (fig. 12b) in the same general locality—such as an entire township or in a whole village.

Apparently, there is no *general* (of wide application) external influence, and the mature, winged adults have been in the colony for some time previous to this "swarm" (which is a colonizing and mating but *not* nuptial flight); they can be induced to fly earlier by disturbing the colony. Can one say the responsible factor is odor or some other stimulus due to developing gonads or sex cells? For these adults do not mature sexually until after the flight.

The stimulus to swarm may be humidity or rainfall in connection with the proper degree of temperature in the case of some termites which live in the earth in arid regions; or hunger in the case of species of *Reticulitermes*, where there is no food taken and the intestinal protozoa that possess enzymes for digesting cellulose—the principal food of termites—have mostly been lost during the final molt, just before the flight. Or are the winged adults forced to migrate by the workers, which with soldiers stand guard at the exits during the swarm? (fig. 12c).

In tropical countries, there is almost an element of magic attendent upon a large termite swarm. Apertures are opened in the ground or parent colony mound and suddenly the air is alive with fluttering winged hordes. After the flight, these exit holes are closed from within by the workers and all traces of life disappear as suddenly as they appeared, the only evidence of the swarm being the discarded wings. Surely the swarm must have been an object of mystery to primitive peoples!

Normally, only *after* losing the wings are the males and females attracted to each other; they then pair off in couples, the male closely follows the female, with head close to her abdomen, stimulated and excited by a sex odor. Together they found the new colony by excavating a small cell or royal chamber in wood, under bark, or in the earth under wood lying on the ground, or in the earth. In the Kalotermitidae sex attraction is evident *before* the loss of the wings, and the males and females *sometimes* do not lose the wings until after they are established in a cell under the loose bark on trees. According to Fuller (1915), in certain African species of *Termes* the winged females settle on grass stalks and engage in a "calling attitude" to attract the males.

Coition is not by superimposition but is effected with male and female on the ground and the abdomens end to end (as in the roaches). Coition does not occur during the swarm flight, nor until the new home is established. The rate of egg-laying is at first slow in *Reticulitermes*, but more rapid in *Termopsis;* and the young parent adults feed and care for the offspring until enough of the workers or nymphs have been reared to care for the needs of the colony. Coition is continued at irregular intervals and the male continues to cohabit with the female for life.

The workers and soldiers of the first

brood that are reared in these nascent colonies are smaller than normal; this dwarf condition of the sterile castes in incipient colonies, or "nanism," is probably due to the scarcity or the character of the food and to the care when the caste system is just developing. Hence, although food both quantitatively and qualitatively may be a factor influencing size and rapidity of development, it has no rôle in determining castes.

Eggs are laid singly, except in *Mastotermes*, where they are extruded in a mass somewhat similar to the oötheca of roaches. The eggs receive the same care from the workers (are licked and tended) that is later given the young or nymphs. The development of the eggs is facilitated by temporary shifts to more favorable locations in the nest. Before hatching the eggs swell up perceptibly.

Only in the case of *Cryptotermes cavifrons* Banks of southern Florida among Nearctic termites, have eggs been found in special cells outside of the royal chamber; here eggs were observed in small separate pockets in fluffy wood fibre in an infested log. In tropical termites (*Termes* group) there are special "nurseries" for the young, recently hatched nymphs.

While queens of the higher termites are larger and lay more eggs, they are normally monogamous, whereas primitive termites are more often polygamous.

The young or nymphs are always active except for relatively short quiescent or molting stages. According to Cleveland (1926) the young or nymphs contain intestinal protozoa 24 hours after hatching, showing that they are being fed by the workers or nymphs (from the ani) and are not eating wood; later they eat wood. The mature soldier, with elongate mandibles, cannot eat wood and is fed by the workers.

There is a remarkable post-adult growth in both the male (or king) and female (or queen) as the colony increases in numbers, much more marked, of course, in the female (fig. 2). With the increase in the number of the egg tubes and actual cellular divisions and growth there is a correlated degeneration of the jaw muscles in the post-adult queens of all types. They lose much of their body color, no longer fly nor eat wood, and according to Fuller (1924), the fasciculate muscles of the thorax become degenerate. They are at this time dependent on the workers, who feed them special food from the mouth. Kings and queens may live together for as long a period as 25 years at least in artificial colonies. Old queens lose some of the segments of the antennae, tarsal joints, margins of the thorax and some body cuticle; these are possibly bitten off by workers or nymphs in their eagerness for exudate.

In well-established parent colonies of *Reticulitermes* in the eastern United States large numbers of nymphs of brachypterous and apterous reproductive forms seasonally appear each year. These forms mature at the same time as do the macropterous adults, and pass through similar molts during quiescent stages of relatively short duration, during the last of which the females (in *Reticulitermes*) lose the abdominal styli—an immature character in the female; hence they are now really an *adult caste*. In apterous reproductive adults in *Archotermopsis* and *Termopsis* the styli are *not* lost in the females. Unlike the macropterous adults, at the time of their flight the sex cells of brachypterous adults are ready to function, and they have lost their intestinal protozoa. Cleveland states that while he is not sure that these protozoa are ever entirely lost in *Termopsis*, they are at least very greatly diminished. In *Reticulitermes* protozoa disappear entirely perhaps at about the

time when the sexual organs begin to function.

Just before the flight of the winged adults, these brachypterous and apterous reproductive adults disappear from parent colonies. What happens to them? Are they killed by the workers in the parent colonies when they are not needed? Or do they migrate to form new colonies? But little is known of the biology of the brachypterous or apterous reproductive adults or castes and how they establish new colonies, which some of them do. Probably these forms migrate with workers or nymphs and soldiers for purposes of colonization through subterranean passages and are impelled by the same stimuli as are the winged colonizing adults.

Sometimes adults of both sexes in species of *Reticulitermes* engage in a short "pseudo-flight" at the same time that the winged adults are swarming. Brachypterous adults come out from the parent colony into the full sunlight and run about, or make slight short jumps or flips into the air—as do the deälated adults—and often they fall over backward in efforts to escape if disturbed. Possibly this activity is a manifestation of or a reversion to the ancestral habit of swarming, or colonization by flight.

These incompletely pigmented, brachypterous adults have the compound eyes reduced and the facets but slightly colored; with the simple eyes or ocelli they are probably able to perceive only light and direction. In *Reticulitermes* they contain (as adults) no intestinal protozoa and hence are dependent on workers for food in order to live. If in the Mastotermitidae and Kalotermitidae these brachypterous and apterous adults contain no protozoa and if workers are absent in Kalotermitinae, nymphs of the sexual adults or of the soldiers must necessarily accompany them in this migration in order to feed them. Cleveland, however, has shown that protozoa occur in these reproductive adults when workers are not present.

Moreover, contrary to the condition in species of *Reticulitermes*, in species of *Hodotermes* (s.s.), *Anacanthotermes*, *Archotermopsis* and *Termopsis* the female adult apterous reproductive forms do *not* lose the abdominal styli in the final molt; hence there also may be differences in the manner of their colonization. These styli are absent in mature, egg-laying, macropterous queens in species of *Archotermopsis* and *Termopsis*, but are present in this same form in species of *Hodotermes*, except in *Macrohodotermes*.

Adults of the apterous reproductive forms in species of *Reticulitermes* have but little color to the body (less than in brachypterous adults) and there are but traces of eyes, whereas in *Prorhinotermes*—as in the lower Kalotermitidae, especially *Termopsis*—there is a marked color to the body and the eyes are merely reduced. Probably only the completely pigmented, winged, colonizing adult with completely developed compound eyes is able to perceive images.

Very little is known of the manner of colonization of these apterous adults or of that of the "intermediate" reproductive forms sometimes found in colonies in a regular series from forms with long wing pads (as in the nymphs of the winged forms) through forms with wing pads decreasing in length to nearly apterous forms. Usually, however, these intergrading forms are not present in such a series in colonies.

At the time necessary for brachypterous and apterous reproductive forms to leave the parent colony, workers (or nymphs) and soldiers would be attracted to these reproductive forms by the exudate, since much of the care of reproductive forms, brood and eggs by workers is due to the

fact that they derive food in the form of exudate from body secretions. In turn, they feed the adults and young, and care for the eggs. This exchange of nourishment explaining coöperative relationships of the termite castes is termed *trophallaxis* by Wheeler.

In nature, in some colonies in the Rhinotermitidae and Termitidae, a single macropterous male may be found associated with numerous egg-laying brachypterous females, the latter forms being probably utilized only because of accident to the macropterous female. That is, occasionally there is interbreeding between the different types of reproductive forms within the species in nature. Unfortunately nothing is known of the resulting progeny. In other colonies both egg-laying brachypterous females and apterous females (rarely) have been found associated together in a small colony; it is to be regretted that no associated males have been found.

No doubt in nature where one or both parent reproductive forms are lost, young reproductive forms present in the colony as nymphs are utilized in replacement. Furthermore, the development of these nymphs in an emergency doubtless is hastened by special care and feeding by the workers.

The larger macropterous reproductive adults normally are monogamous and have greater individual egg-laying capacity; the brachypterous and apterous forms are normally polygamous, but are smaller, with lesser individual egg-laying capacity; however, since large numbers of egg-laying females of the latter types are associated with a relatively small number of males, their collective power for increase in the brood is greater than that of the macropterous forms.

The results of all of the rearing and breeding experiments that have been carried out indicate that no winged adults are produced in *pure* colonies where either brachypterous or apterous reproductive forms were the parent adults. These experiments were of from six to twenty-five years' duration and were conducted with species in several genera in the Kalotermitidae and Rhinotermitidae. Apparently these forms *breed true to type* and produce only workers and soldiers in addition to their own type of nymphs. The sexual forms take two years to develop, and in colonies of *Reticulitermes* in the United States do not appear in the first brood. Workers mature within one year, from the egg to adult, but probably do not have as long a life as the reproductive forms. From a large-headed nymph, they pass through a series of molts and quiescent stages to the adult condition.

The soldiers also mature in one year, they are few in number in the first brood and in fact always relatively few in number. Soldiers pass through a series of molts and quiescent stages from a dissimilar, worker-like prototype to the adult soldier. The change from worker-like form to soldier occurs fairly late in the development or ontogeny of the soldier caste and after this penultimate molt the soldiers, with mandibles merely for defense, never eat wood, but are fed by workers; intestinal protozoa are present as in the worker-fed young. Soldiers do not eat wood directly because they can not chew it; they are fed wood by workers and nymphs. Just how much digestion has occurred before the soldiers obtain the wood is difficult to determine.

In addition to the symbiotic relationship between termites and their intestinal protozoa, which are present in all castes in the families Mastotermitidae, Kalotermitidae and Rhinotermitidae only while they feed on wood, there are numerous insect scavengers, and various grades of insect,

arachnid and other animal "guests" or inquilines in termite colonies. These Hemipterous, Lepidopterous, Coleopterous, Dipterous, etc., inquilines range from persecuted, through tolerated, to protected, remarkable physogastric forms. The inquilines of termites have received much study by entomologists, and Emerson has extensively studied their ecology. Peculiarly modified hymenopterous parasites have been found in colonies having inquilines present which undoubtedly are their hosts; these forms have been described by Brues, Cushman and Rohwer.

In Panama in the carton tree nests of the termite *Microcerotermes arboreus* Emerson, a very peculiar Coccinelid beetle is a cared-for guest. The larvae of this beetle (*Ortalistes rubidus* Gorham) are specially modified and are in the galleries with the termites except when in the pupal cell; they make the same convulsive jerky movements as do the termites, but the adult is of the ordinary type and is not modified.

There is an interesting ecological association between the termite *Nasutitermes cornigera* Motsch. and stingless bees (*Trigona nigerrima* Cresson); in Panama these bees build their nests and honeycomb within the carton tree nests of the termites, often in the center and taking up a large part of the termite nest. Any one disturbing the termite nest is assailed by swarms of these bees which, while they do not sting, bite, and are able to penetrate under clothing, into hair, etc., and make one very uncomfortable.

Certain species of termites (in the genera *Leucotermes*, *Serritermes*, *Nasutitermes* (l.s.), *Anoplotermes*, *Microtermes* and *Mirotermes*, etc.) sometimes live in the nests of other termites. The nest affords both protection and food if they are scavengers or robbers. However, they have separate galleries or smaller supplementary nests of their own and never intermingle in the same nest; if they use the same galleries there is at once a fierce battle.

Further studies of these peculiar, often oddly shaped inquilines will be useful in plotting geographical distribution and relationships; apparently they do *not* occur in termite colonies in the West Indies. The basis for this symbiosis is trophallaxis or exchange of nourishment. The physogastric inquilines receive the same type of food as do the termite reproductive forms. What is its effect? A chemical study of the composition of this special food and a physiological study of its effects might prove both interesting and instructive.

Aside from predators, chief among which are the true ants, termites have no internal insect parasites, which may be explained by their protected conditions of life, the absence of resting stages and their constant activity.

Nematodes and fungous parasites occur and may result in somewhat decreasing the spread of termites. Mites are common externally on termites.

The workers and soldiers exhibit peculiar more or less synchronous, convulsive or jerky movements of the whole body when they are alarmed at a disturbance of the colony, especially noticeable when the reproductive adults appear to be in danger; this movement may also be exhibited by some of the insect inquilines. In some termites a noise is made by the soldiers by striking their heads against wood; in others, the soldiers make a noise by clicking their mandibles. It seems probable that there is some correlation between these movements and noises, and the sense organs, which are located on the antennae, bristles and hairs and pores on the legs, etc. Termites appear to be rather sensitive to vibration; seldom are

they found infesting railroad ties over which there is heavy traffic or in the woodwork of factory buildings where heavy machinery in motion would cause vibration.

Stokes (1893) has made morphological studies of the sense organs of termites and McIndoo (1923) and Hartwell (1924) have studied not only the morphology of these organs but also conducted experiments with particular reference to the location of the olfactory sense; but little is known of sense organs of termites and their reactions to various stimuli. Body odors, as well as odors related to sex, certainly have an influence on activities in the termite colony; there is a distinct acrid nest odor. Body odor, as well as contact stimuli, aid blind worker and soldier termites to maintain a single file formation (as in *Anoplotermes*) outside of the main nest; it enables them to run a straight course to a source of food and might account for other activities sometimes grouped under the heading "spirit of the colony."

Is it not possible that termites have sense or chordotonal organs located on the antennae, bristles, or at the base of the mandible enabling them to receive and respond to vibration stimuli sent through the *air*, or organs located on the legs to receive such stimuli through the earth? May a system of wireless telegraphy especially adapted to these blind insects exist? Of course these convulsive movements may be merely individual reactions, but the fact that the insects are blind leads one to suspect that they are a means of communication. However, what is needed is experimentation, not speculation!

Clark of the U. S. National Museum states: "I imagine that the sound, presumably with a wave length too short for us to hear, does not go either through the air or through the earth, but instead sets up a corresponding vibration in the air pockets between the particles of which the nest is composed.

Air pockets of just the right size would vibrate in unison with any vibration that was attuned to them. Their vibration would set others in motion and thus the sound would instantly travel throughout the entire nest, indicating at once the position of the disturbance.

Organs on the legs would pick up these vibrations much more readily than organs in any other situation.

The use of resonance chambers is probably widely spread in the animal world, though there is practically no mention of them in zoological literature. In some owls the ear region of the skull is greatly enlarged with a peculiar blind pocket outside the ear openings covered by the flap. This seems to be a resonance chamber."

VIII. THE NESTS OR COLONIES

In the lower and intermediate termites, as a rule, the nests are diffused, not well-defined, and more or less temporary; colonies in these nests are more subject to migration due to unfavorable conditions. Among the higher termites, nests are concentrated and more permanent.

In the Mastotermitidae the nests are diffused and in logs or fence posts with galleries in the earth; but no species of the Kalotermitidae (except in *Hodotermes*) burrow in the earth; their nests occur on the surface in logs and stumps and far above the earth in trees and in buildings. In the Rhinotermitidae, species also (except *Prorhinotermes*) burrow below the surface of the ground where they construct a labyrinth of subterranean galleries. In species of *Coptotermes* in Australia, more or less tall concentrated mound nests are constructed above ground, while in species of the same genus in Panama, sim-

ilar nests are below ground; these are exceptions to the general rule of diffused nests among the Rhinotermitidae.

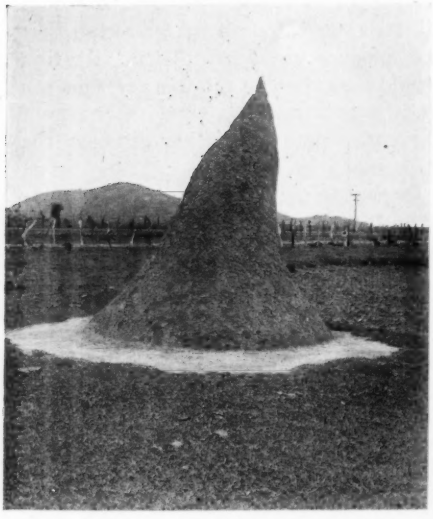

FIG. 6. HARD MOUND TERMITARIUM OR ANT HILL OF *Armitermes medius* BANKS, 8 FEET TALL, 7 FEET IN DIAMETER AT BASE

Note the 12 feet in diameter zone cleared about the mound. April 13, 1924, Panama. J. Zetek, photo.

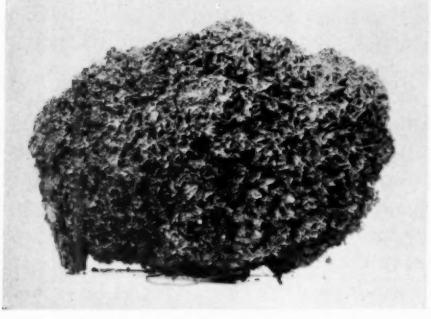

FIG. 7. CARTON NEST ON GROUND OF *Armitermes chagresi* Snyder

Barro Colorado Island, C. Z., Panama. February 21, 1924. J. Zetek, photo.

Among the Termitidae, there are subterranean nests, very lofty or low mound nests (fig. 6) on and below the ground level and carton nests (fig. 7) on the earth or low or high upon the trunks of trees (fig. 8).

In the United States, there are no conspicuous mound nests or arboreal "niggerhead" or carton nests made by termites; nests of our native species are hidden within wood or below ground and termites are seldom seen except at the time

FIG. 8. "NIGGERHEAD" ARBOREAL TREE NEST OF *Nasutitermes ephratae* HOLMGREN, ABOUT 3 FEET BY 2½ FEET ON TREE

Barro Colorado Island, C. Z., Panama. August 22, 1923. J. Zetek, photo.

of the swarm. A key to these Nearctic termites is given on pages 88–9 Bulletin 108, U. S. National Museum.

Family Kalotermitidae

Species in the family Kalotermitidae are wood-inhabiting, being destructive wood-borers in both coniferous and hardwood timber, and do not burrow into the earth, hence they are termed non-subterranean in habit. There is no permanent

true nest and colonies are "diffused" and not concentrated. These colonies live in the moist or dry wood of dead trees, logs, stumps, or in scars or dead areas in the trunk or in dead branches of living trees; or, more rarely (*Neotermes*) in the living wood of living valuable fruit and timber (teak) trees, in fence posts, telephone and other poles, and the woodwork and furniture of buildings. Sometimes colonies are found in driftwood along the seashore and along river banks.

FIG. 9. CHAMBERS AND GALLERIES OF SPECIES OF KALOTERMITIDAE CUT ACROSS THE GRAIN OF WOOD

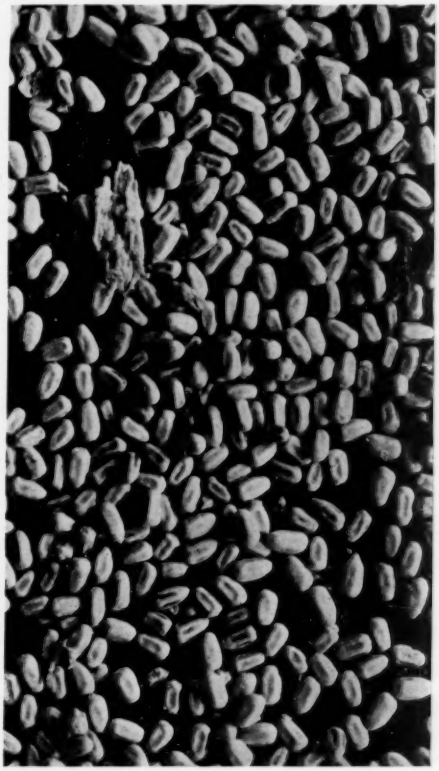

FIG. 10. IMPRESSED PELLETS OF FINE, DIGESTED, EXCRETED WOOD OF SPECIES IN THE FAMILY KALOTERMITIDAE; THESE PELLETS FALL FROM WOOD AND ARE AN INDICATION OF INFESTATION.

The largest Nearctic species in the genus *Termopsis* are not very injurious. The burrows or galleries of Kalotermitidae in wood are longitudinal chambers connected by tunnels; these chambers and galleries are cut across and do not follow the grain of the wood (fig. 9). Pellets of partly digested, excreted wood (fig. 10) fill the

galleries and chambers and often fall from infested wood, indicating the presence of the termites.

In certain genera, the species are able to live in dry, seasoned wood; such termites are called "power-post" termites and are potential "house termites;" they are very injurious to woodwork and furniture and may be carried abroad in furniture, and become cosmopolitan in so far as conditions of climate are suitable.

The reproductive forms are active and do not reach large size; they are able to move about freely in the colony and are not located in a definite chamber or "royal cell;" in consequence they are difficult to find. The presence of slightly larger runways to permit the passage of the egg-laying queens, with their abdomens slightly distended, indicates that they are nearby. Also large numbers of eggs in certain portions of the nest, or the localized presence of more soldiers than normal, often betray their proximity.

FIG. 11. MAP SHOWING WHERE TERMITES IN THE FAMILY KALOTERMITIDAE ARE FOUND IN THE UNITED STATES

Both brachypterous and apterous reproductive forms occur in colonies of species of various genera in the family Kalotermitidae, the frequency of occurrence of a certain type varying with the genus. The brachypterous forms have definite color to the body and slight color to the reduced compound eyes but usually have vestigial, shorter wing pads than occur on this type in the Rhinotermitidae; they are especially short in *Termopsis*, where the apterous form and forms "intermediate" from apterous to brachypterous are more common in colonies than is the brachypterous. The apterous reproductive forms have marked color to the body and slight color to the reduced compound eyes. While rare in *Kalotermes*, this type is common in *Termopsis*.

Species in the family Kalotermitidae can not migrate far and in winter do not burrow into the earth but merely penetrate more deeply within the wood in which the nest is located. Often such colonies in logs, stumps and trees are covered with ice and snow during winter.

Twenty termites in the family Kalotermitidae, representing four genera, occur in the United States; these species are found from Norfolk, Va., to Florida, westward through southern Georgia, Louisiana, Texas, New Mexico and Arizona to the Pacific Coast, where they range northward to Vancouver Island, B. C., (see map, fig. 11) and southward into Lower California.

Family Rhinotermitidae

Colonies of species of the family Rhinotermitidae are excavated in wood near or on the ground; these termites are also destructive wood borers penetrating the hardest of woods, but in addition, they excavate a labyrinth of underground passages in the earth usually near wood or vegetation; they are essentially subterranean in habit, except *Prorhinotermes*, and must have a connection with the earth—the source of moisture so necessary to their life. There is no true permanent nest, as a rule, and colonies are more or less diffused throughout the wood of dead trees, in stumps, logs, scars in the trunks of living trees, fence posts, telephone and

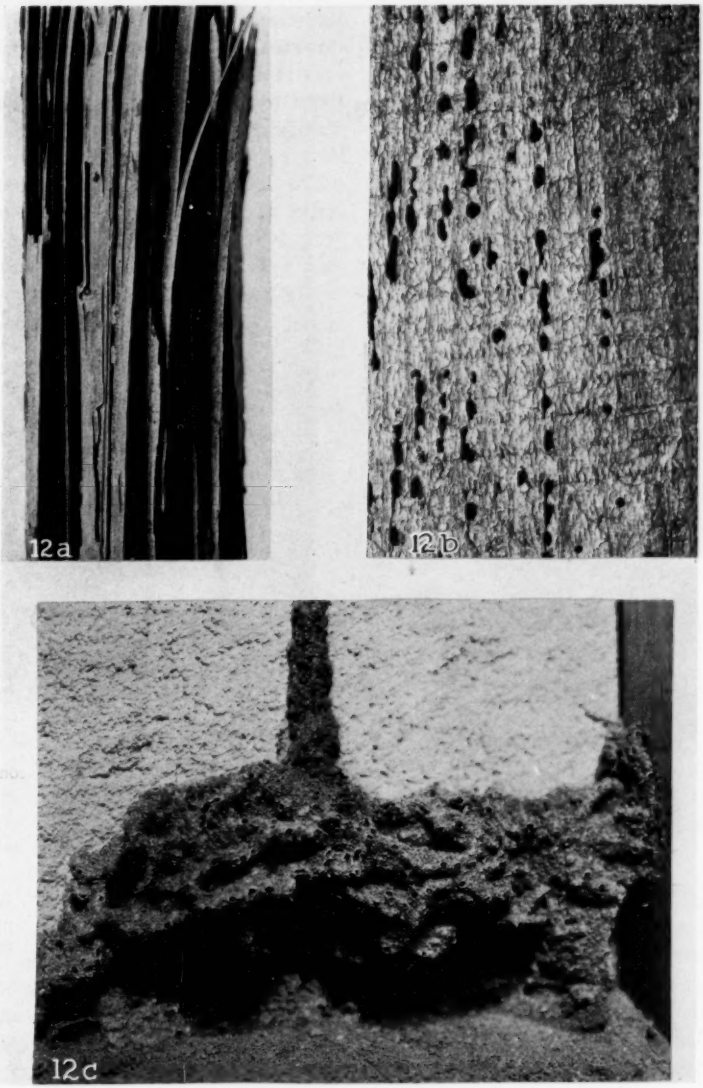

FIG. 12

(*a*) Timber in a building in New Orleans, La., reduced to the consistency of paper; the softer layers of wood have been eaten leaving the harder; i.e., the wood has been honeycombed by a species of *Reticulitermes*, in the family Rhinotermitidae, where the grain of the wood is followed; (*b*) exit holes of winged adults of *Reticulitermes* from pine beam in infested building, Washington, D. C.; (*c*) exit holes in earth-like shelter tubes on wall of infested building, the heads of workers can be seen at the openings.

other poles, and in the foundation and woodwork of buildings. Periodically inundated regions are unfavorable for these subterranean termites, but colonies are occasionally found in drift-wood. Colonies of the non-subterranean species of *Prorhinotermes* are found commonly in swamps. The galleries of these termites follow the grain of the wood, which they "honeycomb" by eating away the larger celled, faster growing wood tissue, leaving the smaller celled denser wood untouched (fig. 12). Living trees and other vegetation are damaged by species in the family Rhinotermitidae, especially by species of *Leucotermes* and *Coptotermes*, which injure valuable fruit, forest and shade trees as well as growing crops. Metal, stone, brick or concrete and other substances which these termites can not penetrate are bridged over by means of granular, earth-like, shelter tubes of small diameter. Sometimes these shelter tubes are suspended from beams (fig. 13) or constructed upright from the floor. Usually they are on some surface such as a wall or tree trunk and often are extended for great heights.

The reproductive adults are not very active and have a remarkable post-adult growth to accomodate the enormous egg tube development. Queens move about slowly but the males or "kings" are more active and usually are not found, since, while they consort with the queen in a semipermanent semblance of a slightly enlarged royal cell, they quickly desert the queen when the colony is disturbed.

In temperate regions, before winter comes, the whole colony (in *Reticulitermes*) leaves the wood and burrows into the earth below the frost line, where they

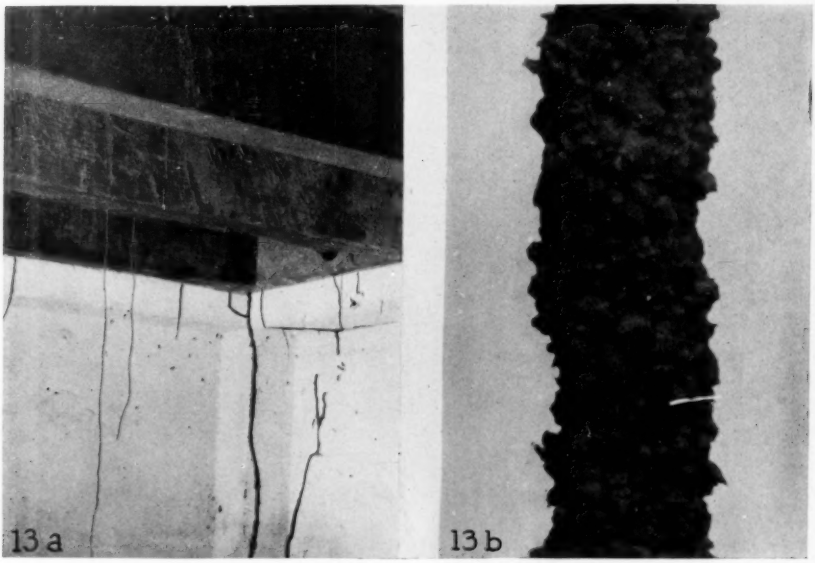

FIG. 13

(*a*) Shelter tubes suspended from beam in ceiling by *Leucotermes convexinotatus* Snyder (Ancon, C. Z.); (*b*) Enlargement of tube (J. Zetek, photo).

normally remain until spring, although they may temporarily come above ground during warm weather. Indeed colonies readily migrate; they change their location within the wood according to the season or with temporary changes in temperature or moisture and even the entire nest may be moved to a new site if conditions become unfavorable. In the prairie and desert regions, during periods of drought in summer when the soil is hard baked and deeply cracked, the entire colony lives in deep subterranean galleries.

In addition to the single pair of male and female reproductive adults developing from the winged forms, there are other types, namely brachypterous adults or forms with short wing pads and with more or less color to the body and eyes—its intensity varying with the genus,—(brachypterous adults are absent in *Prorhinotermes*) and apterous forms; in *Prorhinotermes* and *Rhinotermes* apterous adults have marked color to the body but no color to the eyes. If these adults are the parent reproductive forms, instead of there being merely a single pair, there are large numbers of females with a few males, and instead of all being in a single cell, they may be distributed throughout the colony in a series of broad cells. While these queens do not reach the large size attained by the macropterous adults, there are more of them in a colony. The queens may be located as in the family Kalotermitidae, and are often in the harder wood (such as in knots), in the interior, or in the more inaccessible portions of the wood.

In the United States, there are 12 species in the family Rhinotermitidae, representing 3 genera. These termites occur from Canada to Florida, throughout the central west, along the southern borders of the Great Lakes, and in the Rocky Mountains and Pacific Coast region. Species in one genus (*Reticulitermes* Holmgren) occur in nearly all the states, and represent the most destructive termites in this country.

Family Termitidae

Nests of species in the highly specialized family Termitidae are located in similar places to those in the family Rhinotermitidae, namely, in wood and in the ground; some species are destructive wood borers, while others are essentially subterranean in habit and feed on vegetation in the form of plants; still others live in arboreal nests. Species of Termitidae when wood-boring in habit burrow through both decaying and sound wood; like the species of Rhinotermitidae, they require more moisture for life than do some of the Kalotermitidae.

Apparently as a rule, although their diet appears in nature to be of the same character as that of the Rhinotermitidae, they contain no intestinal protozoa that aid in the digestion of cellulose. Only in a few exceptions (species of *Armitermes*) do species of Termitidae appear to subsist on a more broken down cellulose in the form of more decayed wood or partially digested excreta. However, species of *Reticulitermes* sometimes have a similar diet. Living vegetation is injured by some of these higher termites, including trees, general vegetation and crops.

The macropterous (deälated) queens are usually in a chamber or "royal cell" (fig. 14) and are very large, inactive and practically imprisoned.

While numerous brachypterous reproductive adults of smaller size and with incompletely colored body and eyes occur, as well as "intermediate" reproductive adults, apparently no apterous adults exist; brachypterous adults are especially common in the genera *Armitermes*, *Nasutitermes* (l.s.) and *Microcerotermes*.

In the family Termitidae in the tropics,

colony life, nests and food reach the highest specialization. In general, no intestinal protozoa are present in symbiotic or helpful relationship in species

Among the over-specialized fungus-growing termites, in addition to the royal chamber where the large queen—a mere egg-laying machine—is kept in a protected

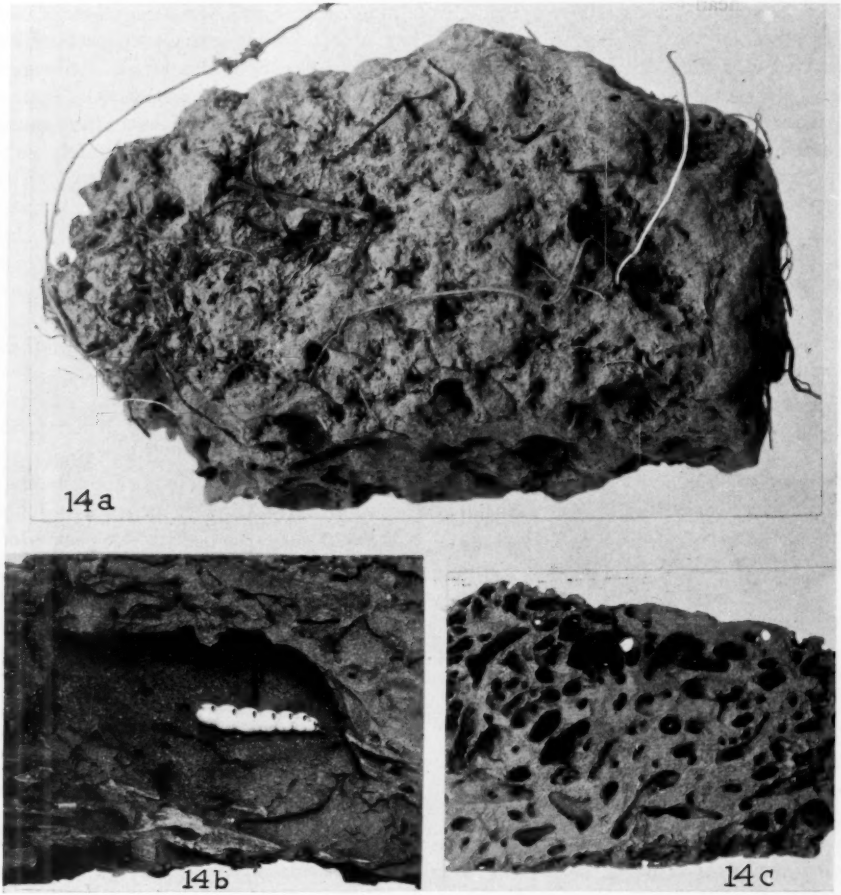

FIG. 14

(*a*) Carton nest or termitarium of the termite (family Termitidae) *Microcerotermes exiguus* Hagen in Panama (September 7, 1923. J. Zetek photo); (*b*) Royal cell with deälated, macropterous queen in cell; (*c*) section of termitarium to show structure.

of this family. Huge, hard, mound nests, and carton nests on the ground and high or low on trees (fig. 14) are developed. Earth-like shelter tubes often are seen as a network on the trunks of trees (fig. 15).

portion of the nest—practically imprisoned—there are special "nurseries" and "fungus gardens," where the fruiting bodies of fungi are eaten. Some of the Termitidae are foraging and harvesting in

habit and their morphological modifications show a regressive development.

Apparently the more protected and concentrated the nest and specialized the food, the larger and more inactive is the queen. In the diffused nests of lower and intermediate termites the queens are small and inactive. In species of *Termes* are found the largest queens, but in the carton nests of *Nasutitermes* and *Microcerotermes* the queens are relatively much larger than in diffused nests.

In the species *Mirotermes panamaensis* Snyder in Panama the galleries in wood are very characteristic, the wood being eaten away in a lattice-like design. Mound-like, earth-like, carton nests are made on the ground or the species inhabits logs, stumps and branches on the ground or decayed places in living trees. The macropterous (deälated) reproductive forms are in a special nest-like carton structure if the nest is in the wood of trees; in one large colony nine females and one male were found together; the queens averaged only 6.5 mm. in length and 2.65 mm. in width. Soldiers of *Mirotermes* make a peculiar clicking noise with their elongate mandibles.

Mirotermes panamaensis is one of the few species in the family Termitidae to have possibly symbiotic protozoa in the intestines; it contains a large amoeba that ingests wood, but that apparently is not in symbiotic relation with its host.

Cleveland has proved (1923–1926) that in the lower and intermediate termites these protozoa possess enzymes for digesting cellulose, the chief food of termites. Protozoa are also found in the intestines of another Termitid (a species of *Nasutitermes*); both *Mirotermes* and *Nasutitermes* are wood feeding termites and possibly obtain their protozoa through association in wood with other termites (Kalotermitidae and Rhinotermitidae) which normally contain intestinal protozoa. If such be the case, which is greatly to be doubted, the theory of a possible correlation of the phylogeny of the protozoa with that of their host termites might be weakened. According to Kirby, the amoeba in *Mirotermes* could not have been obtained by associating with species of

FIG. 15. COVERED RUNWAYS ON TRUNK OF CUBAN ROYAL PALM MADE BY *Microcerotermes* SP.

Ancon, C. Z., Panama. J. Zetek, photo. These shelter tubes extend from the ground to a carton nest on the side of the tree.

Kalotermitidae or Rhinotermitidae, since in none of the latter are any amoebae present; it came from none of the lower termites unless all these species have since lost amoebae. Despite records to the contrary, it can not be certain that there were not small amoebae and flagellates in those species of Termitidae which are recorded as free from intestinal protozoa.

For it is practically impossible to find these forms in specimens of termites preserved in alcohol. Hence, according to Kirby, it is not advisable to state arbitrarily that intestinal protozoa are absent in the highest termites—the Termitidae.

The problem of possible transfer of protozoa between species of termites is extremely important. However, the habits of termites do not suggest this possibility in nature, except where different species of termites inhabit different portions of the same nest, which is a comparatively rare occurrence (see page 540) under "Biology of the Termite Castes."

In the United States 10 species of Termitidae occur, representing 4 genera or subgenera. They live in wood and in the earth and do not construct mound or carton nests. Like the species of the Rhinotermitidae, they require considerable moisture for favorable conditions of life. Species of *Tenuirostritermes* in the southwestern states damage living vegetation by nocturnal foraging expeditions conducted by the workers and nasuti.

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AGE AND AREA

By J. C. WILLIS, F.R.S.

[The Quarterly Review of Biology has no intention of boring its readers with polemics. But the attack on the Age and Area hypothesis in an earlier number presented such an extremely one-sided view of the matter that it seemed desirable to restore the balance. Accordingly we have asked the distinguished originator of the theory of Age and Area, Dr. J. C. Willis, to prepare the following article. We now intend to give our readers ample time fully to digest and assimilate this two-course meal before offering them any more *pabulum* flavored with Age and Area.—The Editor.]

ABOUT four years ago, under the above title (from the principal thesis therein brought forward) I published a book which has aroused some controversy and much criticism. Whether my views be accepted or not, they have reawakened interest in the fascinating study of geographical distribution, which for a long time has been in undue abeyance, and much new and valuable work has been brought out.

My principal thesis, "Age and Area," is based upon *statistics*, whose introduction into biological work is sometimes resented, though one is becoming used to their employment in Mendelism, in agricultural research, etc. Many years ago, Hooker published a statement to the effect (14, vol. i, p. 438) that "All seem to resent the making botanical geography too exact a science; they find it far easier to speculate than to employ the inductive process. The first step to tracing the progress of the creation of vegetation is to know the proportions in which the groups appear in different localities, a relation which must be expressed in numbers to be at all tangible." My work has consisted largely in following up this suggestion, and in showing in what manner the careful use of statistical methods can be applied to aid the various ways—morphological, ecological, and other—already in use for the investigation of the complex problems of botanical geography.

My statistics, which might otherwise have been dismissed as those of an amateur, have received great support from the fact that they have been taken up by the well known statistician Mr. Udny Yule, who has based upon them an important paper (33).

As I have pointed out in the first sentence of my book, "The existing distribution of a plant (or animal) upon the surface of the globe, which is often a very complex phenomenon, is due to the interaction of very many factors;" and at the end of the same paragraph I have said, "To all this it is obvious that age must be added—the older a species is, the more area will it have had time to cover." People have often taken up Age and Area *alone*, as if it, without assistance from other branches of knowledge, were expected to provide a master-key that had only to be turned in the lock to open a main avenue to the solution of the problems of geographical distribution. These problems are among the most complex and puzzling of all that arise in biology, and without the application of all the various criteria that are available —morphological, cytological, ecological,

and all the rest must also be applied—Age and Area will only lead to disappointment. Too much is expected of it, and because it alone will not explain the distribution of a family like the Magnoliaceae, that has passed through many geological periods, and many climatic and other vicissitudes, or explain the limited areas of such local endemic species as those of the Gulf of St. Lawrence, or the scattered woody endemics of parts of the United States, it is rejected as valueless. I have not laid stress in my papers on the employment of these other criteria because I have taken it for granted.

DEVELOPMENT OF AGE AND AREA

It may be well, as a preliminary, to consider briefly how "Age and Area" was arrived at, and matured, after some twelve years of work upon the flora of Ceylon. I very soon noticed that the local endemic species, which make up some 27 per cent of the flora, were rare—a very remarkable fact when they were (at that time) supposed to be specially adapted to the local conditions. Trimen, the author of the Ceylon flora, divided them into six classes, VC, C, RC, RR, R, and VR (very common, common, rather common, rather rare, rare, and very rare), largely by the extent of their distribution in the island, except that VC and C covered the same areas, the former being commoner upon the ground. If one unite these two, one gets five classes. To verify my final statistical results, obtained by adding up the whole flora, I took the flora of New Zealand (Cheeseman), using actual longitudinal measurement of range in these long narrow islands, and made ten classes. Adding these together two by two, one obtains five, to compare with the Ceylon figures. Dividing the Ceylon flora into (1) endemic, (2) occurring in Ceylon and South India, and (3) going beyond this, and the New Zealand flora into (1) endemic, (2) wides reaching New Zealand only, (3) endemics reaching the islands round New Zealand, and (4) wides doing the same, one gets the following table:

CLASS	CEYLON			NEW ZEALAND			
	(1) E.	(2) C.S.I.	(3) W.	(1) E.	(2) W.N.Z.	(3) E.I.	(4) W.I.
1	104	168	683	112	74	62	70
2	128	114	313	120	54	15	9
3	133	87	209	184	36	11	7
4	190	66	159	190	26	5	4
5	232	79	144	296	23	5	4
Average rarity...	3.4	2.7	2.1	3.4	2.3	1.7	1.5

The wides are most numerous at the top, the endemics at the bottom, and the columns are *graduated* from one end to the other. In other words, the wides are the most widely distributed in Ceylon, the species occurring in South India next, and the endemics least. In New Zealand the wides that reach the outlying islands are most widely distributed, the endemics that do the same are next, and then follow the wides that do not, and the endemics that do not.

Now such figures as these are very striking, and they require explanation, especially as similarly graduated figures turn up in a number of other cases. There must be some reason for their graduations, and for the great differences shown by the various classes of plants, endemic or other. Statistics, as these are, are quantitative data, affected by many factors, but when they show a definite graduation like this, there is most probably to be seen the effect of one factor—alone, or principally. Now it is all but impossible to suppose that these figures show the effects of adaptation, or of natural selection—these would

hardly be nicely graduated. It is open to anyone to propose any explanation of them, but so far the only other explanation than mine is that they are due to pure chance. This however does not explain why wides and endemics differ. My explanation is that *on the average of numbers of allied forms* (for the figures show in the same graduated and differential way for single families or for large genera) the effect may be broadly put down to age. Age in itself effects nothing, but it represents the resultant effect of all the various forces that are acting upon the distribution—dispersal methods, adaptation to climatic and biological factors, progress of the association to which the plants concerned happen to belong, and so on. If one suppose that the wides of Ceylon are the most widely distributed there because *on the whole* they arrived first in the island, the South Indian species next because they arrived *on the whole* later than the "wides," and the endemics least because they were *on the whole* evolved later still, one obtains a conclusion which fairly well explains all the facts that are to be seen in the statistical tables. But these are general results, only valid for groups of allied species, and quite inapplicable to individuals. Many endemics will have been evolved in Ceylon before all the wides have even arrived there, and will have reached the maximum degree of commonness. Other endemics will have been evolved upon isolated mountain tops, and even though very old will not have spread beyond their first location. But on large numbers the facts come out clearly enough.

Finding that similar statistical results appeared in many different floras, I drew the general conclusion that Age and Area was applicable, not only to one country, but to the world; but one must always deal with matters in a statistical way, and not try to apply conclusions to small numbers. Similarly, finding that in the statistics, size of a genus went with the area occupied, when one took them in groups of allies, I formulated the rule which I have called Size and Space.

GENERAL ANSWER TO CRITCISM

I. Constant conditions

A great deal of adverse criticism has appeared, and it is not altogether easy to understand why Age and Area has met with so much reprobation. That if more time be allowed for the active factors in distribution to carry on their work, more area will be occupied, seems a very harmless and all but self-evident proposition, and it was clearly put forward by Grisebach, followed by Lyell and Hooker. As I have pointed out (AA, p. 6) "the *resultant* effect of all the active factors, like dispersal methods, etc., is so uniform, when one considers long periods of time, and takes an average of several allied species, that these species spread indefinitely at a fairly steady average rate. This rate . . . . will probably not be the same for any two species, but for allied forms will not usually differ very much, so that by taking groups of ten allies, and comparing with other groups allied to the first, the rate of expansion of area will be a fair measure of age."

The general answer that may be made to criticism is that the hypothesis is based upon statistics, and must be handled *quantitatively*, and that the provisos with which I have hedged it about must not be ignored. Yule defines statistics as "quantitative data affected to a marked extent by a multiplicity of causes." Only by taking numbers can one hope to perceive any result that one may interpret as due to one of these causes, and one must always deal with numbers if one hope to get results of any value. For some inscrut-

able reason, the fact that I have made provisos at all seems to arouse hostile criticism. Had there not been these provisos it would have been so easy to upset the hypothesis, and though my critics often begin by mentioning the provisos, they usually end by ignoring one or more of them, and sometimes all, completely.

On page 63 of my book, the hypothesis is thus stated: "The area occupied (determined by the most outlying stations) at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man, and by other causes."

Now most of my critics are inclined to lose sight of these provisos, upon which I have always insisted. If they be neglected, it is easy to find facts that are quite incompatible with Age and Area, and special attention must once more be called to them. The first is "so long as conditions remain reasonably constant." It is of course all but impossible for them to remain exactly constant, but they may be much the same on averages of say ten years, and so long as that average does not show a steady and marked change in one direction, I should class the conditions as reasonably constant, though the rainfall, the sunshine, the ecological conditions, etc., may vary from month to month or from day to day. Such conditions occur, for example, in the great tropical forests, in the moorlands of Europe, in the deserts of the southwest United States or in the Yellowstone Park, places where man is not continually interfering with his agricultural, warlike, and other activities, and where the secular change of climate is extremely slow.

It must of course be remembered that the chief obstacle to rapid distribution is probably the presence of definite associations of plants over large areas, but even here, as Clements says, "the most stable association is never in complete equilibrium." Here the changes of conditions are going on more or less in a definite direction, but so slowly that I think one may regard the conditions as reasonably constant.

Careful adhesion to this first proviso renders nugatory many of the criticisms that have been made, for my critics have taken the case of plants that have gone through many vicissitudes of climatic and other change, like the plants of the Gaspé region, which have at any rate been more or less surrounded by ice on one or more occasions, or the family Magnoliaceae, which have survived many changes. In such cases, Age and Area *alone* can give no result that is worth consideration, unless one can trace by aid of the fossils the area that has been covered, and that sometimes twice or more. If plants have been compelled to migrate back and forward by alternations of ice and of warmer periods, the area really covered may be represented by *several superposed folds*, a fact that is usually completely lost sight of. In regions seriously affected by glacial periods, Age and Area may be regarded as inapplicable until we can trace all the migrations, but the nearer to the Equator one goes, the more useful does it become. In the north there are many endemics of very isolated forms, that may be regarded as real relics, but in the equatorial regions these are but few and there are vast numbers of endemic species that are closely related to their surrounding species, whether endemic or wide. These forms enormously outnumber the relics of more

northern countries. H. A. Gleason (7, bottom of p. 544) says that "it is essential to the validity of Age and Area that migrations be always forward." This I fail to grasp, but as I have just pointed out, much must not be expected of Age and Area in regions where migration, usually due to ice action, is common. With the go and come of the ice, a species might easily have migrated three or four times over the same ground, and unless one could trace its progress accurately with the aid of fossils at different levels, one might go very far astray. If the ice advance rapidly, as is often supposed to have been the case, some species will not be able to migrate fast enough to escape extermination, while others will already be so far ahead of the ice, or so rapid in movement, that they will survive. In the Old World there is a vast mountain barrier from east to west, against which many species might be killed out altogether, while in America there is room for migration much further to the south.

Further than this, the oncoming and subsequent retreat of the ice seems often to have made a definite change in the climate and other conditions, rendering life less favorable to the growth of the (generally) woody or arboreous forms that previously occupied the ground, and which, like so many of the local woody endemics in the flora of the United States (*cf.* AA, footnote, p. 86) now survive in the midst of conditions that are generally unfavorable. Since the ice retreated, man has occupied the ground, further increasing the unfavorable conditions.

But it is not only a change of climate that has affected these plants. The invasion of the ice has usually broken up or destroyed the old associations in which they used to live, and in consequence of this, their rate of distribution must probably have become enormously slower than under the old conditions. In fact, it is not improbable that the changed conditions offer a complete barrier to further distribution. In any case, one will not expect to see any serious extension of area unless the old association can be largely reconstructed, or unless the species can force its way into some new association, for which the pioneer species will prepare the way. These endemics, which after all are few compared to the multitudes of non-relic endemics, are local, like the most of the Ceylon endemics, simply because there has not yet been time for them to be anything else, even when they are not checked by the barriers of climatic and other change. But their previous history may be written in the fossils, and must be followed there.

The old idea (encouraged by the rapid spread of weeds in cultivated ground, where the original plant asscciations have been completely broken up) that distribution is very rapid, still holds a large sway, but as I have endeavoured to show (AA. pp 19–22, and Chap. V) there is little or no justification for the taking up of this attitude towards the subject. Distribution in general, over ground more or less fully occupied by associations of plants, will be an extremely slow process, and its does not in the least surprise me that so many plants in various regions of the United States, which must of course be regarded as relics left by the ice age, should still be confined to the places (perhaps a little extended) in which they were left. They are in general surrounded by associations that are probably different from those in which they lived, and one will expect them to spread, if at all, with the most extreme slowness. The present tropical forests go back probably before the ice age, yet they contain many endemics that have only spread a very short distance, though the conditions have been favorable.

One of the things that I am fighting for in my advocacy of Age and Area is to get the idea accepted that distribution is a dynamic process, which is still going on. It is not, in my opinion, a phenomenon that takes place so rapidly that most things have already reached their limits of possible distribution. They have reached so far as age (representing the resultant of all the active forces in distribution) can carry them up to the present time, against the influence of the various barriers—physical, ecological, and the like—that check or oppose their distribution.

This same proviso as to constant conditions of course really disposes of any attempt to consider by aid of Age and Area alone such cases as those of Sequoia and many other plants which have gone through two or more geological periods, for they can hardly have escaped being affected by great changes of conditions during so long a time, and we cannot always say from the fossils exactly what their migrations may have been. Here again, to look upon distribution in a dynamic way will somewhat change our views upon the subject. As I have pointed out (AA, p. 88), there is hardly a more suitable conifer for general sub-tropical conditions than *Cupressus macrocarpa*, which has been planted in millions over the mountains of the tropics, and in other places of like conditions. And yet, if one examine it in its only *native* habitat, one is forced to conclude that it is, *there*, a species that is dying out, on account of unfavorable conditions. Had it not been taken up by man for planting in conditions that are more suitable to its growth, there can be little doubt that it would ultimately have disappeared, and would have been counted from the fossils as one of those species to which the world was no longer suitable. It is not to the world, but to the conditions that have supervened in the regions where they were growing, that species like this, or *Sequoia*, have become unsuited; they have not been able to spread quickly enough to reach more favorable localities, or these may have been too far away to have been reached in any case. As the world grows older, the climate tends to become drier, and shows more differentiation, and this alone has localized many forms that in more uniform climates would have occupied much greater areas. At the same time, differentiation of species seems to accompany differentiation of climates, and as Hurst has shown with regard to *Rosa* (16), the original species, carrying the possibilities of resistance to different types of climate, seems gradually to differentiate into species suited to one only.

A careful taking into consideration of my first proviso is thus a sufficient answer to many criticisms. How closely, even in the far north, recent species, evolved since the conditions became pretty much what they are now, may follow the rule, may be seen from the work of Samuelsson (22), who shows the way in which endemic plants—in this case *Hieracia*, and evidently of recent formation—spread from centers where they are (at present) comparatively numerous, and occupy scattered locations round about. His map of the distribution of one of these microspecies, here reproduced, shows this very well, giving the actual spots in which it has been found in a country well worked for *Hieracia*. The further one goes from the center of distribution, the more scattered become the locations, and Samuelsson also remarks (reprint, p. 6). "In den Standorten an den Grenzen des Verbreitungsbezirkes scheint die Anzahl der Individuen kleiner als im Centrum zu sein. Mindestens ist dies der Fall in Dalekarlien, wo zwei Standorter bekannt sind." This is what

one would expect, on the general principles which I have endeavored to make clear in Chapters II to V of my book. The more closed the associations of plants become, the slower will be the dispersal, but every now and then a species will get a foothold in a new place, often, it may be, at a considerable distance from any other members of the same species. In the map just given, the most isolated locality is separated by about 20 miles from the next, though of course one cannot be certain that there is not, and never has been, an intermediate position.

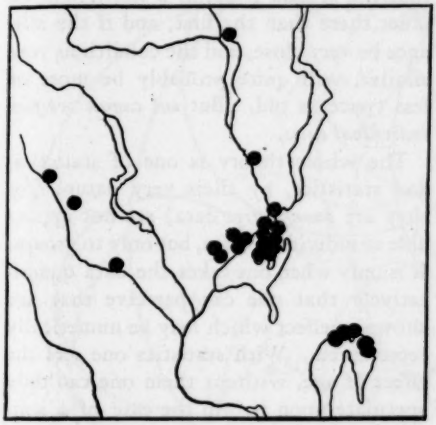

DIAGRAM A. Distribution of *Hieracium chloroleucum* Dahlst.

On page 10 Samuelsson goes on to explain this remarkable distribution, and says "ist meiner Ansicht nach das geringe Alter jener Sippen die wichtigste." Here then is another anticipation of my detailed publication of Age and Area, though my own first suggestion of it was in 1907, and as I have pointed out in my book (p. 3), Lyell and Hooker published the general idea in 1853, whilst Samuelsson points out that Grisebach (9), six years earlier, calls attention to plants that are so young that they have not yet had time to be distributed far from their point of origin.

Samuelsson points out that the conditions in much of southern Sweden are practically the same as those where these very local species at present exist, and that there is no reason to suppose that they would not succeed over much larger areas than those which they actually occupy. He also points out how often single plants or clumps of individuals of new and distinct forms have been found, and have never been found again, in spite of much searching. He takes the same view of this as I have taken in my book upon page 151, that the collection of the specimens exterminated the species, a view which Dr. Guppy has also proposed to me to account for the many species only once seen, and never found again.

Samuelsson then goes on to point out that the distribution of these *Hieracia* negatives the idea that it can be in response to an adaptation to local conditions (*cf.* AA., pp. 231, 148, 87, etc.). and that though they are obviously very young, no intermediate forms can be traced, even in the case of such a very local form as *H. microcymon*, which he regards as evolved since the arrival of man in Sweden. He regards the forms as having arisen by mutations, and says "Das Alter der Sippen der *acroleucum*-gruppe scheint der Grösse der Verbreitungsbezirke ungefähr proportional zu sein. Es ist deswegen wahrscheinlich, dass *H. acroleucum* die älteste Sippe dieser Gruppe ist. Vielleicht sind alle übrigen Sippen der Gruppe aus *H. acroleucum* entstanden." This is the point of view that I have taken for many years (*cf.* 26–29) and which I am once more bringing up in recent papers (30). The original idea goes back at least to G. St. Hilaire, and, as is well known, species were always supposed to arise suddenly in the days of special creation.

The gradual development of them is an assumption brought up by Darwin and his supporters in this matter, and is as yet without proof.

Samuelsson also suggests that some of the very isolated localities may be due to another appearance of the same mutation, a possibility that appears not improbable when one has realized for example the way in which the mutant *gigas* appears again and again in de Vries' cultures, or considers how likely it is that the same change in the nuclear constitution may happen twice, especially perhaps in nearly related forms such as these *Hieracia*.

Samuelsson's whole paper is very interesting, and deserves to be more widely known. He ends by pointing out, with a map drawn from Wettstein's own localities for gentians (23), that the latter's widely accepted opinion, that species arise as adaptations to local conditions, and do not overlap, is not sound, for there is in fact considerable overlap. The maps agree much better with the view of origin by mutation, and gradual dispersal from the centers of origin. Arguments based on Wettstein's published opinions require careful examination with the facts.

II. Consideration of groups of allied species

The next proviso in my statement of Age and Area is as important as the one which has just been considered, and though from the very beginning I have strongly insisted upon it, it is very often ignored by my critics. It is that one must always deal with "*a group of allied species at least ten in number.*" This again disarms much of the criticism that has been directed against Age and Area. Practically all the local woody endemics mentioned above for the United States, for example, or those of the Gulf of St. Lawrence, are rendered valueless for purposes of argument, inasmuch as they cannot be placed with the needful number of allied forms to make up a group of ten close allies—in many cases they cannot even be placed with others of the same family—nor are there other ten, nearly allied to them, with which to make a comparison. This point, too, I have especially insisted upon (*cf.* AA. pp. 85–6). If a group of ten allied *Dipterocarpus* trees, for instance, cover an area (sum of all ten areas) of 100,000 square miles, and another group of ten allied to the first, and in the same country, cover 200,000 square miles, then Age and Area indicates that the second *group, as a whole*, will be older there than the first, and if the alliance be very close, and the conditions very similar, will quite probably be more or less twice as old. But *one cannot compare individual cases.*

The whole theory is one of statistics, and statistics, by their very nature (for they are *quantitative* data) are not applicable to individual cases, but only to groups. It is only when one takes the data quantitatively that one can perceive that age shows an effect which may be numerically represented. With statistics one sees the effect of age, without them one can only speculate upon it. In the case of a solitary individual species, so many factors are operative, that the effect of no single one can be picked out with certainty, though all kinds of speculative or theoretical views may be put forward as to the causes that have operated to produce this or that effect. But when one takes large numbers, and finds the totals varying in a direction that seems only explicable as the effect of age, then one becomes justified in proposing age as an important factor in distribution, and in pointing out certain results as being probably due to it. The results that show very clearly with large numbers also show so well with smaller numbers, when one takes close allies and

compares them with other allies, closely allied to the first, that one is also fairly justified in fixing a number like ten as a minimum. But these ten *must* be closely allied, and *must* only be compared with other groups of ten allied to the first. The exclusion of individual cases from consideration throws out at once a great proportion of the objections that have been brought forward.

Individual species differ so much in their reactions to the surrounding conditions that probably no two are distributed at the same rate, except at times accidentally, and to reason from the hypothesis of Age and Area for an individual species, or even for a group of two or three, is wholly to misunderstand the principles underlying statistics and their use.

Let us take the very simplest case that it is possibly to imagine. Suppose that ten species of a genus *A* all commence *in the same country at the same moment* X, and another ten of a genus *B*, as closely allied to *A*, and as much like it in every way, as possible, all start at the same moment Y. The problem before us is to determine which moment, X or Y, was the earlier, assuming the correctness of Age and Area. Let us further suppose that each species has spread uniformly round its point of origin, so that we

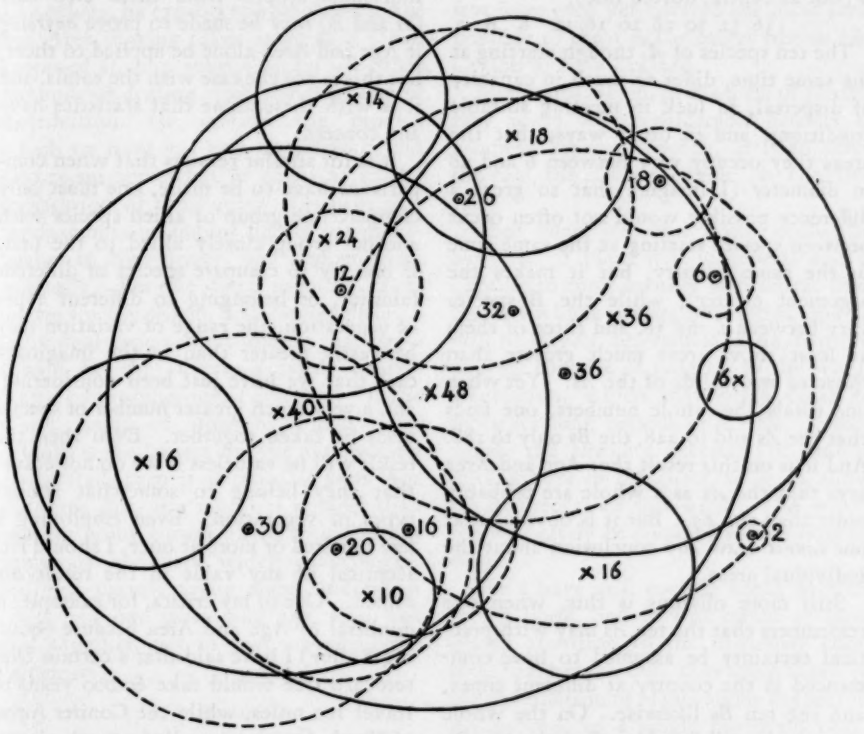

Diagram B. (For explanation see text)

can work with the diameters of the circles thus formed. Then we begin by measuring the diameters of the various circles, which look a hopeless intermixture. Arranging them in order of size, we get the result

A (cross at centre, solid line):

48 40 36 24 18 16 16 14 10 6

B (dot at centre, dotted line):

36 32 30 26 20 16 12 8 6 2

The ten species of *A*, though starting at the same time, differ so much in capacity of dispersal, in luck in meeting suitable conditions, and in other ways, that the areas they occupy vary between 6 and 48 in diameter (I imagine that so great a difference possibly would not often occur between species starting at the same time in the same country, but it makes the argument clearer), while the *B* species vary between 2 and 36, and three of them at least show areas much greater than those of two thirds of the *A*s. Yet when one totals the whole numbers, one finds that the *A*s add to 228, the *B*s only to 188. And it is on this result that Age and Area says that the *A*s as a whole are probably older than the *B*s. But it is obvious that one *cannot* draw any conclusion about the individual areas.

Still more obvious is this, when one remembers that the ten *A*s may with practical certainty be assumed to have commenced in the country at different times, and the ten *B*s likewise. On the whole the ten *A*s will be older than the ten *B*s, but beyond that Age and Area cannot go with any probability of safety. It is obviously impossible to reason—one can only guess—about the individual species that make up the tens.

This explanation will, I hope, help to make clear the general statistical principle upon which Age and Area is based. The explanation upon page 62 of my book should also be read in this connection. In my earliest papers I fixed at 15–20 the number of allied species with which one ought to deal, and I am not sure it might not be safer even now to return to these figures. Or perhaps it would be more correct to say that the further one goes from the equator the larger the number that one should use. Individual species from these two lists (*A* and *B*) may be made to prove *anything* if Age and Area alone be applied to them, but this is not the case with the totals, and it is with these alone that statistics have any concern.

It is for similar reasons that when comparisons have to be made, one must only compare one group of allied species with another group closely allied to the first. If one try to compare species of different families, or belonging to different types of vegetation, the range of variation may be vastly greater than in the imaginary case that we have just been considering, and a very much greater number of species must be taken together. Even then the result will be valueless if we do not ensure that they belong to somewhat similar types of vegetation. Even employing a few hundred or more at once, I should feel sceptical of any value in the result obtained. One of my critics, for example, is doubtful of Age and Area because (quoting Ridley) I have said that a certain Dipterocarp tree would take 60,000 years to travel 100 miles, while the Conifer forest of North America travelled a much greater distance in much less time. But the two groups are in no way related, have different types of seed, and live in different countries and conditions, and *cannot* be compared. A note in *Science Suppl.*, March 3, 1926, p. x, gives figures for dispersal of seeds of the Douglas fir. Unfortunately the height is not given, but Ridley's tree was 100 feet, and while he found that even in strong wind the seeds

did not go beyond 100 yards, the fir seeds, in an eight-mile breeze, fell in maximum quantity at 360 yards, and some overpassed the observers at 530 yards. Groups of plants must be compared, and even then only the closest relatives, living in closely similar conditions.

A paper by Calvert (2) illustrates this disregard of my provisos, and shows that like others, he expects too much from Age and Area, having taken it up as if I had proposed it as a substitute for all other methods of dealing with the problems of distribution. He ignores the proviso which we have just been considering, and also seems somewhat in doubt as to the application of the figures. On page 221, for instance, he quotes figures for distribution in New Jersey, and applies them generally. On the next page he takes figures for the world, and applies them to individual genera, thus finding that *Argia* should be the oldest—a result contradicted by morphological evidence. If the whole group of allies to which *Argia* belongs is the largest and the most widely distributed, then it is probable from Age and Area that as a whole it is older than another group closely allied to it and less numerous and less widely distributed. But one cannot argue about individual cases, and one must take age, size, and area together, not in two separate compartments.

III. Barriers

We now come to the reservation about *barriers*, that the action of Age and Area may be enormously modified by their presence. This is obvious in the case of sea, for only a few species are occasionally and with difficulty able to pass across any serious width of salt water (cf. Guppy's books). "For the case of floras (plants in ecological association) Dr. Willis rightly insists that land connection, complete or all but complete with the source of dispersal, at the time of dispersal, is necessary" (Mrs. Reid, AA, p. 139). This can hardly but be admitted by anyone who has studied the subject. An endemic, starting, as so many have done, upon an island, has only the very remotest chance of ever spreading beyond the confines of that island; though, as a matter of fact, few have even yet covered the local areas possible to them in the larger islands like Ceylon or New Zealand.

Mountains, again, in the form of chains, may afford very considerable barriers to progress, especially when, as is so often the case, the climates differ on the two sides.

Then there are the many ecological barriers. A plant will in general find it difficult to enter another association than that to which it usually belongs, and so will be largely determined in its distribution by the rate of progress of the whole association, which may often cease to move for long periods at a time. Hence again, the absolute necessity of dealing with groups of ten allies, so as to allow for differences of this kind. The whole ten will rarely be confined to one association.

But I have said enough about barriers in my book, and it will suffice to have drawn attention to the obviously enormous differences that they may make in the distribution of plants about the world. An endemic of a single mountain peak, extending some distance above the general height of the chain, may easily be barred from ever extending beyond it, if it is not suited to life at somewhat lower levels (cf. Gleason, l.c.).

In what has been said, I hope that I have made it clear that one must work with great caution and circumspection in applying the rule of Age and Area. Some who have now contemptuously rejected

the whole thing have taken it up as if it had been proposed as a master-key to the problems of distribution—as if it were to be simply a case of "measure a few areas and there you are," leaving morphological, ecological, and other criteria out of consideration.

Some systematists hold the opinion that because what were once accepted (by such masters of systematic botany as Hooker, for example) as general species, ranging enormous areas, are now being split into smaller species of more limited range, Age and Area can no longer hold. As I have already pointed out (AA, p. 98, objection 29) such work really strengthens the position of the hypothesis. The more local the species "become," the more clearly do they show the effects of age in their dispersal (cf. the work of Samuelsson, already referred to). The local species that are thus made out of the wide-ranger are more closely related to it than to others, and the whole goes to show the truth of Guppy's deductions as to the breaking up of the widely ranging species into local forms—the process of differentiation. As I have said (28, p. 135), "isolation, *as isolation*, favors the production of new forms." It is impossible for me to go over every one of the thousands of species with which I deal, to determine its latest systematic position; one is reminded of the Scarabee's remark, "Cuvier had to go to Latreille for his insects, and if Latreille had been able to consult me—yes, me, gentlemen[5] he wouldn't have made the blunders he did about some of the coleoptera." My opponents treat statistics in a very cavalier way. I say that statistics show for example that the average Scot is heavier than the average Englishman, and they reply in effect "Oh that's absurd, for here is Smith weighing 180 pounds and McKenzie only 140."[5]

RECENT PAPERS

A considerable number of papers, in favor of, or opposed to, Age and Area, have been published during the last few years, and it will be well in conclusion to deal with some of these, as illustrating points that have not been dealt with in the general reply to objections that has been made above.

My views are sometimes objected to, on the ground that they seem to imply that the number of species is tending to increase rather than to remain constant, and it is therefore of interest to find that G. R. Wieland, in the fifth chapter of "Organic Adaptation to Environment" (Yale University Press, 1924) shows that the view which is very frequently put forward, that previous ages have had vast numbers of species, lacks good evidence to rest upon. He points out that as yet only about 12,000 well described species of fossil plants are known. Berry makes the number 20,000, but even this is but small beside the number of living species. Wieland thinks that at the beginning of the Cretaceous 40,000 species of flowering plants may have existed in the world. Only the Pteridophytes and the Gymnosperms, of living classes, have gone down in numbers since the Permo-Trias, and all the rest have increased. He then calculates the rate of evolution from these figures, and comes to the conclusion that one species in 80 years would be sufficient—a figure which offers an interesting comparison with my estimate of one in 50 years, and Mr. Yule's of one in 15 to 30 years.

Miss Chandler has published some very interesting work upon the geological history of *Stratiotes* (3), showing that it has usually been represented by one species only on each geological horizon. The differences between two successive species are hardly explicable otherwise than by

mutation, and they have no apparent reference to usefulness, proceeding for example from a testa with tubercles in rows to a testa with scattered tubercles, and finally to the existing *S. aloides* with none. It is specially noteworthy, however, that the tubercled and smooth forms of *S. aloides* have been found in the same geological horizon, e.g., from samples of the Cromer Forest Bed at Beeston, and it looks as if they might have been in existence at the same time. The impression one gathers is as if the whole species perhaps changed simultaneously, or nearly so, and as one can see no use-relationships in the characters that have changed, there *may* have been some internal force, of an orthogenetic character, regulating it. In this connection, Hurst's work is of very great interest, and will be mentioned below, while attention should also be drawn to that of Rosa (20, 21), though space will not allow of its detailed consideration. According to him, species change over their whole area, tending to continual dichotomous splitting, one new species being rather progressive, the other the reverse. The "future" open to these species becomes continually less and less as the splitting goes on.

Hurst's work (16) goes far towards an explanation of many things that have always been stumbling blocks, providing a new standard for classification, and showing that the species arise in the genus *Rosa* to a great extent by loss of chromosome septets, each septet carrying with it a considerable number of characters. This indicates that the origin of species one from another by single steps—one of the implications of the hypothesis of Age and Area which is strongly supported by the facts of geographical distribution, and for which I have contended since 1907—is a highly probable event. It also indicates that the origin of the same, or very similar species, in two widely separated regions, is by no means an impossible event.

Another geological paper which bears on the subject is that of Woodhead (32). The last paragraph states "These studies of the Pennine Peat indicate that the species found at the base, and presumably the oldest in the area, are the same as exist on the moors today; further that they have now the widest distribution, and extend into the Arctic regions. It is suggested that as the Southern Pennines was an unglaciated area during the Ice Age, these moorland species would for the most part persist through that period. As the ice receded, many of these would serve as efficient colonizers and extend their bounds. Maps indicating their distribution in detail, show that they occupy a larger area than any other group of native species. This generalization also applies to the whole county of Yorkshire, thus from a different line of enquiry supporting Willis's contention of Age and Area, that the plants which occupy the greatest area in a given country, at a given time, are the oldest plants in that area."

Important evidence has also been given by Guppy (11), who shows that the Canary Islands display a double endemism, that peculiar to the group (about 400 species), and that which it shares as a member of the Macaronesian region including Madeira, the Azores, and the Cape Verde Is. (about 50 species). On the hypothesis of Age and Area, the latter will be the older, and in actual fact they prove to be what are often called the Tertiary relics of these islands (though by the way they show no signs of dying out), while the former are endemic species of more recent Mediterranean genera. Not only are the Macaronesian endemics distributed outside the Canaries to the other islands mentioned, but also, just like the

Ceylon-South-Indian species in Ceylon, they are more widely distributed in the Canaries themselves than the younger endemics of Mediterranean forms, occurring on an average in 3.5 islands each, while the latter only occur in 1.7.

He quotes Pitard and Proust as describing the origin of species from the widely ranging polymorphous species: e.g., *Micromeria varia* occurs all over the islands, while there are 15 endemic Micromerias confined to one, 3 to two, and 1 to three islands. He quotes my paper of 1907 (26) in this connection.

Dr. Willey (24) gives an interesting table showing the frequency in capture by townet in the Gulf of Guinea of those Copepods found only there (average frequency 1.8) and those that also occur in the Great Acadian Bight (average frequency 51.7, lowest 5, highest 106). He also finds some evidence of the theory developed by Guppy and adopted by myself that a dominant species of wide range may throw off mutants and continue on its course.

Broekens (1) has carried out a useful piece of work in which Age and Area is put to a test which it may legitimately be supposed to bear, and where it is used in conjunction with morphology and with other lines of work. Taking a middle line with the comprehensiveness of the genera, he finds that the family Onagraceae contains 10 monotypic genera, all confined to warm America, as are also the 7 genera with 3 to 6 species. Taking size of genera as well as area occupied and working with 17 genera, all these therefore may be supposed to be young. There remain 11 genera; of these *Circaea* (7 spp.) is widely distributed through the North Temperate Zone (Europe, Asia, America). *Boisduvalia* (8) is confined to California, Peru, and Chile, and is thus probably younger, though it is not safe of course to draw conclusions from single cases. *Lopezia* (12), confined to Central America, is pretty certainly younger, and probably *Chamissonia* (15) in the United States, Peru, and Chile. Next come *Gaura* and *Godetia* (each 20) chiefly confined to Mexico or California, and therefore quite probably young, whilst *Ludwigia* (20) is cosmopolitan, and therefore probably old. The last four genera are *Jussieua* (40, or if united to *Ludwigia*, as is often done, 60), cosmopolitan in warm countries, and with one species, *J. suffruticosa*, almost covering the generic range; *Fuchsia* (60) in America with a subgenus in New Zealand, and therefore probably also old; *Epilobium* (160), cosmopolitan in temperate and cold regions, with some species of enormous distribution; and *Oenothera* (52), confined to America, and therefore quite probably comparatively young.

From these an application of Age and Area (noting however that one is working with single genera to some extent, which is somewhat risky) picks out the group *Jussieua*, *Ludwigia*, *Epilobium*, and *Circaea* as probably the oldest. All the others, except *Fuchsia*, are confined to America.

Applying next the morphological characters and structure, for example the length of the calyx-tube, he obtains confirmatory evidence that points to *Jussieua* as the oldest genus, especially when *Ludwigia*, which has as primitive characters in many respects, is united to it. Into the further details of this interesting paper we cannot go, but it requires special mention as a good example of work in which Age and Area is temperately used.

Following the general lines of my work upon the various invasions of New Zealand by plants, Matthews (17, 18) has begun a series of papers upon the British flora. Dealing first with the flora of Perthshire, he points out how the various species show graduation into progressive

arithmetical series, like the flora of New Zealand. At the first glance, they do not seem very regular, but if one separates the alpines from the lowland plants, this difficulty disappears. There are no endemics of course in Scotland, but the figures show their chief concentration at the mouth of the Tay, and it is up that valley that the invasion of the Highlands by Southern forms has proceeded. In later papers he deals with the British flora as a whole, taking in the first the 266 plants confined to England and Wales. These are found to diminish from the southeast in all directions north and west, and the figures become much more regular when divided into four groups, which show their maxima at the mouths of the Ouse and Thames valleys, near to Southampton Water, and in the peninsula of Cornwall. As Mrs. Reid puts it, "Mr. Matthews has proved that though Age and Area on the surface appears to hold not particularly well, it is not because it really fails, but because it is masked by a disturbing cause, and when that cause is discriminated and eliminated, there stands the law fully evidenced."

Matthews' second paper deals with the plants of England, Wales, and Scotland only, and he shows that the southern, non-alpine, forms have advanced in the same way as those of the previous paper, but further, whilst it is no longer possible to determine in detail the number of directions in which they invaded.

Fernald (5) shows that the unglaciated areas of Gaspé and western Newfoundland bear a considerable number of species which are most nearly related to plants of the western Cordillera, Alaska, and Siberia, though separated from them by about 2000 miles. Of these 225 species some 80 are endemic, a large number for a region in latitude 48°N., though small in comparison to the numbers that occur in places of similar or smaller size in more southern regions (Canaries 450, Ceylon 790, Cuba 1000, San Domingo 1050, New Zealand 1200, etc). They show a vastly greater endemism than do the plants, largely of Arctic origin, which have come up into the glaciated regions since the retreat of the ice; a fact which points to their much greater age. They have probably persisted in their present location since preglacial times. In spite of their great age, however, the areas that they occupy are very small, and we are invited to consider this as an exception to Age and Area. But the fact of their extreme localization only goes to show that their rate of dispersal is *very* slow, even if not all but entirely held up by the barrier formed by the change of climate that has occurred. One cannot, as required by Age and Area, add these species together in groups of ten close allies, for they largely belong to different and scattered genera, nor can one easily compare them with other groups, closely allied to the first. They are relics, in general divorced from the associations to which they once belonged, and therefore will find distribution a matter of great slowness and difficulty, while in view of the desiccation that has gone on over so much of the continent it is probable that they are hemmed in by ecological barriers at no great distance, if indeed these barriers are not actually closing in upon them, and exterminating them slowly but surely, just as appears to be happening with *Sequoia*, *Cupressus macrocarpa*, and other plants.

To turn to the last critical paper that I have seen, that of Fernald (6), the first criticism that he makes compares the areas occupied by Dipterocarp trees with those occupied by Conifers, and I have already pointed out that as these groups are quite unrelated they cannot be compared. He then goes on to object because

my statements are taken from books rather than from field work. In general the authors of floras enter the localities of their species, and it is obviously impossible for me to verify them for myself, when I am dealing with thousands of species. If by the constant collection of rarities rather than of common species, the former are made to appear more common than they should, it is surely very remarkable that the Ceylon edemics should still be of a rarity of 3.4 (*cf.* above) against 2.1 for the wides, the New Zealand 3.4 against 1.5 for the wides that also reach the outlying islands.

Knowing by long experience the great divergences of opinion as to the standing of this or that form in specific or generic rank, I have never attempted any criticism of the species with which I have dealt, and any criticism directed against me upon these grounds (and there is a great deal) should be directed against the authors of the floras which I have used. If I criticize one species, I must criticise all, and lifetimes would not suffice, nor would anyone admit that my criticisms were justified. Further, I have pointed out above that species-splitting (I have always followed the general lines of Linnean species set by Sir Joseph Hooker) really lends great support to Age and Area.

Another criticism refers to the work of Prof. James Small, and the latter informs me that, as indeed is clear in his article, he did *not* employ Age and Area in his selection of the Andean region for the origin of the Composites, but his own cartographic method (*cf.* his "Origin and Development of the Compositae" pp. 246–7, 250–51, 257, and *Carpolithus hyoseritiformis* Berry).

The criticism of my use of such papers as those of Taylor upon the endemics of New York is answered by what I have said above, that I exercise no criticism upon what I use. The two families that I have myself studied in the field, giving long periods of time to each species, give very strong evidence in favor of Age and Area, as I have shown (AA, p. 92), and hope to show in more detail in later papers.

In dealing with sizes of genera, Prof. Fernald takes them in a miscellaneous way, and does not compare them each in groups with groups of close relatives, and is again attempting to apply statistical methods to individual cases. If in the world at large six closely allied genera occupy areas (*or* have numbers of species) represented by 10, 8, 8, 6, 4, 3, and six more, closely allied to the first six, by 7, 7, 6, 6, 5, 5, and yet another six, closely allied to both, by 6, 5, 4, 4, 3, 3, then the total areas (or species) will be 39, 36, and 25. From these results I should say that it was quite impossible to decide which of the first two *groups as a whole* was the older, but that both were with some probability older than the third, though six is a somewhat small number to work with. It is quite impossible, however, to place individual genera in order of age, or to compare any genera except with their *closest relatives*. The rules of Age and Area &c cannot be indiscriminately applied, and applied *alone;* they must be used along with all other possible evidence. We know so little about the evolution and distribution of plants that we cannot afford to neglect anything that may help in elucidation. When one comes to a genus like *Carex*, so overwhelmingly larger than its most closely related forms, one is naturally tempted to infer that it may be older than they, but when one adds it to a few close relatives, one does not feel so sure. Taking figures from *Die Natürliche Pflanzenfamilien*, one finds the six Cariceae to average 90 species each, the six Sclerieae 18, the six Hoppieae 5, the

four Gahnieae 17, and the sixteen Rhynchosporeae 20. From these figures one feels inclined to say that the Cariceae are *as a whole* the oldest group, and one must then go on to take the areas occupied, when one again finds them on the average covering the largest areas. But out of the many Rhynchosporeae one can pick as many and as widely distributed genera as the whole of the Cariceae, so that in the end one is led to the conclusion that the Cariceae are probably *as a whole* the oldest of the smaller groups, leaving the Rhynchosporeae out of consideration. But more probably the latter are really more nearly allied to the smaller groups than are the Cariceae, so that it is rather the latter that one should leave out of consideration, looking upon the Rhynchosporeae as not improbably the oldest, as a whole, of the remaining groups. And one must go on to apply all the resources of taxonomy, palaeontology, cytology, and the rest, to the question.

With regard to the protean genera like *Rosa*, the explanation seems to me to lie, with great probability, in Hurst's work upon this genus (16). If confirmed by work upon other similar genera, this work will create a wholly new outlook upon the problems of geographical distribution, while at the same time it affords strong evidence in favour of some of the implications of Age and Area, which are probably one of the reasons why it is looked upon by so many with disfavor. For example, take the differentiation hypothesis, as it has been outlined by Huxley (15), and more fully elaborated by Guppy in various books and papers (especially 12, 13, and 10), postulating a primitive type widely ranging in days when the surface of the earth and the climates were more uniform, and then differentiating, with the differentiation of climates that has gone on, into many other genera and species whose range is less wide, as their age is less great. In some cases the original genus, or something very like it, seems to survive, as with *Senecio* in the Compositae (AA, p. 172), but sometimes it has become broken up as in Monimiaceae. But this whole subject will probably require great revision by aid of cytological investigation. The primary differentiation of *Rosa*, and its adaptation to more differentiation of climates, seems to go hand in hand with the loss of septets of chromosomes, each septet largely carrying with it adaptability to some particular climatic conditions. Hurst's map of the distribution of diploid and polyploid species is very instructive in this connection, showing the greater ranges of the older polyploid species, and the detailed work promised will be looked for with great interest. Incidentally this work also goes to show that it is by no means impossible that the same species—as far as chromosome characters are concerned—might at times arise independently on each of the great land masses, though Dr. Hurst informs me that he thinks that only very rarely indeed would the two be absolutely identical. They would usually be separated as taxonomic species or varieties.

SWAMPING AND DYING OUT

One of the most puzzling problems before us is why so many genera are represented in islands and other isolated spots by endemics only. Within the limits at my disposal, it is not possible to deal fully with this question, which requires a paper to itself. Extermination of the more widely distributed form that was presumably the first to arrive, by dying out or crossing, as suggested by Sinnott, will hardly serve as a general explanation. It is doubtless a parallel case to the presence of so many endemics on isolated mountain tops. In the younger islands, more espe-

cially, the genus is often represented by one endemic only, while in older islands there are often a number, usually closely related, and probably derived from the first. Age therefore, as well as isolation, is evidently a factor in the problem. Miss Chandler's observations on the succession of forms in *Stratiotes* doubtless will come in here, as well as Hurst's work on *Rosa*, and other papers. The problem must remain for the present unsolved.

Another very moot point is the dying out of species. Because I have said that the Age and Area figures give no evidence of dying out, I have been accused of saying that no species die out—a statement flatly contradicted by fossil evidence. Mr. Udny Yule informs me that the result of a probable *average* dying out would be to leave my figures much as they are, with a tendency to pile up at the lower end—a tendency which they do perhaps show already. Miss Chandler's work above mentioned shows how one species may succeed another, and the appearance of endemics only in so many genera in islands &c shows how a species may probably die out in a given neighborhood by a single (or series) mutation. De Vries, in a recent paper (4) has made an incisive study of this question, and Mrs. Arber and others have also dealt with it. Space will not permit of full discussion, but I am rather inclined to think that a comparatively local species may often be killed out in various ways, while a widely distributed species will tend to mutate to local species and varieties. Hurst's work may throw light upon the whole question.

I have sketched this article hastily in response to a request, as for the next few months my editorial and teaching duties will occupy all my time; and there is very much more that might be said, and many criticisms that are left unanswered. In general it seems to me that the objections to Age and Area arise (*a*) from the expectation of a large return for little work, and of a return from Age and Area *alone*, without the assistance of all other lines of work that are available to provide evidence; (*b*) from the misunderstanding of what statistics, or quantitative data, really are, and their consequent misuse by application to single cases, or their great complication by being applied to unallied forms, and (*c*) from a more or less complete ignoring of my provisos about reasonably constant conditions, the use of groups of allied species only, comparison between close allies only, the effects of barriers, and the rest. I have tried to insist upon these upon every possible occasion in my book, but for reasons of space, and the great expense of publication in post-war days, have had to leave comparatively untouched the other disciplines about which I have spoken above. Geographical botany is about the most backward section of our science at the present time, but one may wait too long if one wait till the systematists have arrived at agreement about the exact systematic standing and geographical range of every form, in these days when man is so rapidly transforming the earth, and breaking up the old associations of plants.

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THE PRODUCTIVITY OF LAKES

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FROM the practical standpoint the most important consideration in regard to a lake is its capacity to produce fish, and this is the ultimate aim of all limnological studies. This problem has been attacked from many angles, and a sufficient amount of data on the hydrography, character of bottom, inshore vegetation, phytoplankton and zooplankton and their quantitative determination, as well as their chemical analysis, and on the food of various species of fishes, has now been obtained to render a survey of this field useful. The utility of such a survey is twofold; firstly, to see if there is any single characteristic which can be used as an index of the productivity of a lake, so that this index-characteristic may be tested and its validity confirmed or disproved, and secondly, to see what are the chief deficiencies in our knowledge of the ecology of lakes, so that investigations with the specific aim of supplying the lacking information may be undertaken.

A lake, like every ecological habitat, is a complex of factors, and the productivity of a lake will obviously depend upon the summation of these factors. For this reason the investigation of every limnological factor is of value. It is not necessary for the purpose of this brief paper to discuss all these factors in detail, but it should be clearly stated that nothing which is said in this paper is to be construed as minimizing the value of the very fullest investigation of all the factors of a lake.

An examination of the literature dealing with the productivity of bodies of water reveals a strong tendency in recent years to correlate productivity with the amount of plankton. This is but natural, seeing that the great majority of young fishes, and many fishes throughout their lives, feed on planktonic animals, especially on Entomostraca. The second tendency is to seek to relate productivity to the development of organic detritus on the bottom (Petersen and Jensen, 1911; Adamstone, 1924). Some authors, following the lead of Putter (1909 *et seq.*), have sought to prove that the nutrition of many aquatic animals, including fish, depends, at least to a considerable extent, upon organic substances dissolved in the water. Naumann (1918 and 1921) believes that the chief nutriment of many planktonic animals (Cladocera, Copepoda, Rotatoria) consists of the "seston" or fine organic particles suspended in the water.

It will be seen, however, upon close analysis, that none of the above really get to the bottom of the problem of productivity. In the case of the phytoplankton it is true that a large part of the nutriment they yield is elaborated from carbon dioxide and water by photosynthesis, and it is equally true that the supplies of these two materials, are universally present in water, and the energy (sunlight) used in their transformation to sugars and starch

is likewise universally available. Therefore if the development of phytoplankton depended solely on these factors it should be equally abundant in all waters,—which is not true. It is quite evident that there is some factor which limits the production of phytoplankton, and this factor is undoubtedly the availability of elements which are necessary for the formation of protoplasm, especially nitrogen and phosphorus. In the case of organic compounds, whether present as detritus, or seston, or dissolved in the water, it is quite evident that they are secondary products, and that the manner of their production must be explained if we are to arrive at the ultimate factors in the productivity of lakes.

There is, here and there, in the literature, a suggestion that the rooted aquatic plants play an important part in the productivity of bodies of fresh water. I was led to make a survey of such literature as I had at hand, with this point in mind, by my observations, firstly, that entomostracans were most abundant both as to species and individuals, amid the rooted vegetation of lakes, secondly, that other aquatic invertebrates (protozoans, rotifers, amphipods, isopods, mollusks, insect larvæ, etc) were abundant in such habitats, and, thirdly, that lakes in which I have found an extensive development of rooted vegetation, such as Lake Opinacon, and Burford Lake, were renowned resorts of the angler.

Before giving a brief review of the literature on the rôle of rooted aquatic vegetation it may be well to summarize the various points in connection with the part they play in the economy of lakes.

1. Rooted aquatics, such as *Elodea*, *Potamogeton*, *Vallisneria*, *Myriophyllum*, *Naias*, *Nymphæa*, *Castalia*, *Brassenia*, *Nymphoides*, *Sagittaria*, *Ranunculus aquatilis*, *Bidens beckii*, *Lobelia dortmanna*, *Polygonum amphibium*, *Eriocaulon septangulare*, etc., absorb salts, including nitrates, phosphates and potassium compounds, from the soil (Pond, 1905). When they decay these salts are added to the water, where they are available for the use of phytoplankton.

2. These plants, on decay, add organic compounds to the water, and, as has been demonstrated by Artari, Knorrich, Snow, and myself, organic matter in solution augments the growth of planktonic green algæ.

3. These plants, on decay, contribute very materially to the organic detritus, which not only favors the growth of more plants, but forms the chief food of many aquatic animals.

4. They provide places of attachment for immense numbers of algæ (Chlorophyceæ, Cyanophyceæ, Diatomaceæ), which form the food of many aquatic invertebrates.

5. They provide places of attachment for the eggs of various species of animals.

6. They serve as forage plants for some aquatic animals, such as some insect larvæ (Moore, 1913) and amphipods (Embody, 1912).

7. They provide hiding-places for fish.

8. They tend to hold the soil of the bottom, including the organic detritus, in place, thus keeping it from being carried into water too deep for the growth of rooted plants.

There are two other rôles which are often mentioned in considerations of these plants, and which are sometimes regarded as of great importance, but which I am inclined to regard as negligible in the case of lakes. These are, firstly, that they, by photosynthetic activity, add oxygen to the water. This is, unquestionably, an important rôle in the case of aquaria, and

it may be in the case of small, shallow ponds, but in the case of lakes the water, down to the depths at which such plants grow, is sufficiently oxygenated, chiefly by wind action, to provide for the oxygen requirements of any animals which live in such habitats. The second of these rôles is that "they shelter fish from the heat of the sun." This is, I consider, an imaginary rôle, derived from an analogy to conditions on land, as our studies of the penetration of long-wave-length radiation into water tend to refute this contention.

Of the points mentioned above I consider the first four to be by far the most important, as these phases influence, not merely the local habitat, but the whole body of water.

The following survey of literature on this subject is by no means complete, but the material presented is fairly representative, especially as far as North America is concerned.

Thompson (1896) says that "The flora of Pine Lake is exceedingly meager. The observer may row along its shore for miles without seeing one thrifty bed of waterweeds," and Ward (1896) comments on the poverty of the fauna of this lake.

Lemmermann (1897) says "Ausserordentlich wertvoll für die Fischteiche sind dagegen nach meinen Beobachtungen die Pflanzen mit Schwimmblättern, wie *Potamogeton natans*, *P. crispa*, *P. amphibium*, *Hydrocharis morsus ranæ*, etc."

Embody (1912) speaking of fresh-water amphipods, says "All forms were always found associated with vegetation, living or dead."

Moore (1913) shows that many forms of life are associated with the potamogetons, and says that "The present investigation affords further evidence of the economic value of these plants."

Kofoid's statement (1903) that "The amount of plankton produced by bodies of fresh water is, other things being equal, in some inverse ratio proportional to the amount of its gross aquatic vegetation of the submerged sort" is often quoted, and accepted as it stands. It should be observed that Kofoid was here dealing with *Ceratophyllum demersum*, a non-rooted aquatic which comes into direct competition with the phytoplankton, and not with rooted aquatics which do not so compete for nitrates and other salts.

Galtsoff (1924) says "It has been found that the production of plankton can be considerably increased if the pond is drained and its bottom allowed to overgrow with vegetation. When several months later the pond is again filled with water the zooplankton develops in greater abundance." The only reasonable explanation of this increased productivity lies in the materials furnished by the decaying vegetation, and this statement tends to bear out the contention as to one of the major rôles played by rooted aquatics.

Moore (1920), dealing with the ecology of ponds at the Fairport Fisheries Biological Laboratory, says that in pond 2D "fully one-tenth of the surface has been covered by the large rooted aquatic *Potamogeton illinoensis*," and that this pond produced *Volvox* and *Bosmina* in tremendous numbers, the entomostracan feeding on the *Volvox*. Wilson (1923) says that this same pond, 2D, "contained more than twice as many beetle species as pond 1, and while in the former seven species were abundant and eight were common, in the latter only two abundant and four common." Pond 1D had mats of algæ but no *Potamogeton*. Wilson also states that the *Potamogeton* increased from year to year until it covered one third of the pond, and that "the beetle fauna has steadily increased in number and variety."

Reighard (1913) speaking of the fish communities of Douglas Lake shows that three species are characteristic of the stony shoals, and five species of the deep water, while ten species are characteristic of the submerged vegetation, eight of which are found only amid this vegetation. He also states that two more species—the small-mouthed black bass and the pike—occur at the edge of the vegetation and make frequent forays into it in search of food.

Muttkowski (1918) finds that there is, in Lake Mendota, a far more varied and abundant fauna among the rooted aquatics than in any other habitat.

Baker (1916) says "Plants not only afford a place for support, upon which snails may crawl and find a resting-place, but they are actually eaten as the regular food supply. In view of this fact the statement of Shelford (1913, p. 58) that 'we could probably remove all the larger rooted plants and substitute something else of the same form and texture without greatly affecting the conditions of life in the water, that is, so far as the life habits of the animals are concerned' is misleading."

Baker (1918) under the heading "Submerged Vegetation" says "When it is remembered that each plant harbors a host of animals (mollusks, crustaceans, worms, insects, etc.) it is at once apparent that this abundant plant life forms a primary food supply of great value," and "The greatest development of plant and animal life on the bottom is found within the six-foot contour. Of the 1,164 acres examined about 88 per cent of the individual invertebrate animals were found within the six-foot contour. . . . . When we remember that fish are more abundant within the six-foot contour, where the majority of young fish live and most adult fish breed, the significance of this richness of bottom life in the shallow water is at once realized, and indicates that this is the most important depth for the culture of fish."

Some idea of the quantities of vegetation produced in lakes may be gained from the work of Rickett (1924) who states that from 0.25 of a square metre in Green Lake, Wisc., 2,700 grams (wet weight) of submerged aquatics were obtained.

Needham (1922) speaking of submerged aquatics in Lake George, N. Y., says "In this rich mixture of weeds a very great number of small crustaceans, insects, mollusks, and worms, find food and shelter. They in turn furnish food for fishes."

Adamstone (1923) says of Lake Nipigon "As regards animal life, and particularly Mollusca, the most productive parts of the lake are the small sheltered bays and the channels between islands. This is true, especially where the bottom is covered with sand or mud, on which there is much organic débris to furnish food material." The same writer, (1924) recognizes the importance of submerged aquatics, for among his suggestions for increasing the productivity of Lake Nipigon he includes "Since Lake Nipigon so largely lacks aquatic vegetation, amongst which other investigators have found enormous numbers of organisms, it might be possible to introduce species of plants not already found there or to disseminate more widely those which have already established themselves to some extent."

Evermann and Clark (1920) discuss the rôle of aquatic plants as oxygenators, as shade, as protection and as food. They state that "The vegetarian minnows feed upon plants or plant fragments of appreciable size, and the carnivorous forms feed largely on aquatic insects or their larvæ which in turn feed on the plants. The bluegill, which is largely a vegetarian, feeds directly at times upon the leaves of

pond-weeds (*Potamogeton*), and at other times upon the little crustacean, *Asellus*, which feeds upon the weeds."

The most valuable contributions with which I am familiar towards our knowledge of aquatic vegetation have been made by Pearsall, and the value of these papers lies in the fact that he relates the aquatic vegetation not only to the character of the bottom, but the latter to the geological formations in which the lakes are found, and, on the other hand, he relates the vegetation to the fish of the lakes. Pearsall (1920) says "The distribution of the aquatic plants considered is primarily governed by the nature of the substratum, while the reaction of the substratum to vegetation is controlled by variations in the quality and quantity of sediments deposited on it and by the type and quantity of organic matter it contains." The same investigator (1921) says "This detailed discussion shows clearly that the fundamental factor in the development of the attached vegetation is the increase in abundance and richness of the sediments. Not only does this control the types of plant communities found, but it also limits the quantity of vegetation produced." . . . . "As a lake develops, silts become richer and more abundant, and *rooted vegetation* more luxuriant. Hence there are increased areas on which epiphytic algæ can grow, and increased shelter and food for the smaller aquatic animals." . . . . "It would thus appear that the increase in rooted vegetation, in the bulk of the plankton, and in the abundance of fish, are all changes to be correlated one with another, and ultimately depend upon the topographic development of the lake."

In this latter paper Pearsall touches upon a point in connection with the English Lakes which I have observed in our lakes, that is, that certain fishes are typical of "non-silted" lakes, for instance trout, and others of "silted" lakes, perch, both here and in England, and black bass in our waters. He is not able to give a satisfactory explanation of the absence of trout from the "silted" or evolved lakes, though he suggests "the silting up of their stony feeding grounds" and "summer stagnation." I would advance, as a tentative suggestion, the competition of the perch, bass, and other predaceous fishes which flourish in evolved lakes. Since this is a most important question in regard to fish culture in North America every effort should be made to arrive at definite conclusions concerning it.

Menzies (1925) states that the young salmon (smolts) grow far more rapidly in silted streams than in rock-bottomed ones, and that their growth rate is correlated with the geology of the region in which they occur.

The aim of this brief paper is, as was stated at the beginning, to see if we could get any suggestions as to an "index character" of the productivity of lakes. It would appear that the amount of rooted submerged vegetation *may* be such an index character, and it would seem to be decidedly worth while to see if this conclusion is valid. If it is, we have here an index character which can be "read" far more easily and quickly than factorial measurements or plankton estimations, and this will be of special value in a country such as ours where inland waters are both numerous and spread over a large territory. Moreover, if it is definitely proved, by quantitative studies, that the rooted aquatics play a major rôle in the productivity of lakes it should be possible to introduce them in suitable places, if any such exist which are not yet occupied by them, or even to change limited areas of bottom, by diminishing wave-action or bringing in soil, so as to render such areas suitable for their development.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

A STATIC THEORY OF HEREDITY

Being a review of *The Theory of the Gene* by T. H. Morgan. New Haven (Yale University Press), 1926. 6½ x 9¼; xvi + 343. $4.00.

By Julian Huxley, King's College, University of London

The very title of this book provokes to historical reflection. Some biologists have fought against the term *gene* because it recalled Darwin's hypothesis of pangenes, that edifice of speculation which the great naturalist, as he himself wrote, felt constrained to advance in spite of the absence of any confirmation in fact, because of the imperious need which his mind felt for some intelligible mechanism of what was then the "great mystery" of heredity. Today, not only has the word *gene* come to stay, but Morgan can quite justifiably give his book this proud title, safe in the assurance that the theory of the gene is now as fundamental for biology as is the theory of evolution itself, something which in spite of possible modifications will always have to be reckoned with as an integral part of the science, like the theory of stratigraphical succession for geology, or the atomic theory for chemistry and physics.

Put in most general terms, a theory of genes implies a particulate theory of life. It implies that the hereditary constitution of organisms is not an indivisible whole, but an organization of units or factors which can be taken apart and recombined in very various ways, in precisely the same way as, on the atomic theory, a chemical compound is not something indivisible, but an organization of units which can be taken apart and recombined in other ways.

There have been a great many other particulate theories of life. But all these were alike in being the purest speculations, incapable of confirmatory test, merely *ad hoc* explanations. Weismann's great edifice of theory comes in a slightly different category. True that his ids and determinants were wholly speculative entities; and true that it has turned out that these particular speculations were incorrect. But at least he did attach his speculations to something tangible, by locating his units in the newly-investigated chromosomes; and this guess has proved to enshrine the truth.

Meanwhile Mendel had taken the first step towards the modern theory of the gene. He had demonstrated that, in

certain cases, the inheritance of visible characters depended upon invisible factors, which must be units, must be separable from each other and must behave in a precise and regular way, capable of being prophesied beforehand. On the other hand, he failed (because of technical difficulties which he could not then appreciate) to extend his results to certain other forms. Naudin had also attained very similar results, but not only did he also fail to generalize them, but they were never as clear-cut as Mendel's, and his proof of the existence of unit-factors was never rigorously complete.

There the matter rested for nearly forty years. Bateson was on the verge of discovering the existence of unit-factors for himself, when their existence, in Mendel's work, was re-discovered in 1900. It was characteristic of Bateson that he never dreamt of pressing his claims to independent discovery, but himself became the protagonist of Mendel as the founder of a new branch of science. From that day, only a bare quarter of a century ago, to this, progress has been rapid. Looking back we can see that there have been four or five main advances, each demanding a period of years. It will clarify our perspective to recall them.

First there was the extension of Mendel's ideas to all kinds of organisms and all kinds of organic characters. In this, Bateson was the protagonist, and the second edition of his *Mendel's Principles of Heredity*, published in 1909, may be taken as marking its close. By then it could be clearly seen, by all those with eyes to see, that the existence of hereditary unit-factors was not an isolated or exceptional fact, but was the rule in at least all higher animals and plants.

Arising out of intensive and extensive survey came, as was inevitable, a modification of the original simplicity of Mendel's two laws. Bateson and Punnett discovered what we now know as linkage. They also discovered mutually-interacting factors, multiple factors, incomplete dominance, reversal of dominance, and other complications.

Meanwhile, quite independently, progress had been made along the line already taken by Weismann of linking on the invisible hereditary factors to the visible machinery of the chromosomes. Sutton very early put forward the view that Mendelian factors were located in particular chromosomes; this was ably defended by numerous other cytologists, particularly in America, but convincing proof was lacking.

The close of the first decade of the twentieth century was marked by notable advances. Johannsen in Denmark clinched Weismann's views on the need for distinguishing between inherited germinal variations and non-inherited somatic variations, by his beautiful analysis of variation in pure lines in beans. Doncaster discovered sex-linked inheritance, and was quick to connect it with the cytological facts concerning sex-chromosomes.

Here closes the second chapter of Mendelism. The next chapters alter the character of the theory itself and inaugurate what we may call neo-Mendelism. The great advances here fall in the second decade of the century. They begin with the discovery of *Drosophila* as an ideal genetic material, and are due chiefly to Morgan, Bridges, Muller and Sturtevant, working in collaboration at Columbia.

The two outstanding achievements of this period are, first the definite and final proof that the chromosomes are the bearers of Mendelian factors; and second that particular factors are situated in particular chromosomes and at particular positions within these chromosomes, so that the

hereditary constitution begins to appear as a set of definite units, arranged in a definite way in space, and existing in definite quantitative proportions. The most spectacular piece of work of this period was the mapping of the chromosomes.

Another great advance of this period was the discovery of hereditary variations due to the subtraction or addition of whole chromosomes, first discovered by Gates, or to the subtraction or addition of whole genomes (complete single sets of chromosomes) as in haploid and polyploid individuals. The most beautiful applications of the first principle have been made by Bridges in his studies of non-disjunction, and of the latter by Wettstein in mosses, while Blakeslee has demonstrated both in operation on the grand scale in *Datura*.

The final great advance concerns the nature and action of factors. This may naturally be subdivided into two more or less separate lines of work, one concerning the relation of factors to other factors, the other concerning their relation to the process of development.

As regards the first, here again the studies of *Drosophila* have been all-important. In the first place came the studies on multiple allelomorphs, which demonstrated that one and the same gene could exist in a whole series of related forms, almost invariably causing a graded series of visible effects. Then came the discovery of true modifying factors, whose visible effects will only be produced if certain other genes are also present to be modified. Most fundamental of all, Bridges was able to prove up to the hilt (what one would have thought was *a priori* to be expected, but was as a matter of fact not generally accepted), that the sex chromosomes exerted their effects not *per se*, or as it were *in vacuo*, but only when in a certain relation with other chromosomes.

Drosophila, of course, has two similar sex or X chromosomes in the female, an X and a Y in the male. At first it was generally supposed that the X carried the factor for femaleness, the Y that for maleness. Later when the Y chromosome was shown to be without any sex-determining power at all, it was supposed that one X inevitably produced a male, two X's a female. However, Bridges has now conclusively shown that sex-determination is an affair of balance or proportion between X-chromosomes and autosomes; whenever the number of sex-chromosomes is equal to or greater than that of autosomes ($X:A \geqq 1$), the type is female; whenever it is equal to or less than one-half that of the autosomes ($X:A \leqq 0.5$), the type is male; while when it is about two-thirds of the autosomal number ($X:A = 0.66$), intersexual types are the result. Thus animals with 3 sets of autosomes are female if they have 3 X's, as also are haploid animals with one set of autosomes and one X.

Starting from this point, the extremely fundamental theory of 'genic balance' has been formulated, according to which a gene's effect (quite apart from changes in the environment) depends upon the other genes with which it is connected in the hereditary constitution.

There appear still to be some biologists who attack Mendelism on the ground that it is a preformationist doctrine. There was never much ground for this view: no serious Mendelian ever supposed that a factor was in any way a miniature replica or even representative of a single character. Today there is no ground whatever. The term *unit-character* itself has been almost entirely dropped, for the simple reason that characters cannot be "units;" and we have reached a position precisely

similar to that of the chemists in regard to the atomic composition of matter, or to that of philosophers like Whitehead in regard to the structure of objects in general. The hereditary constitution is not only composed of units in particular proportions and arrangement, but its effects are determined by these proportions and this arrangement just as much as by the particular nature of the units; this standpoint is identical with the chemist's. The properties of water are not those of hydrogen and oxygen added together; but only hydrogen and oxygen combined in a particular proportion will give these properties, while the same elements combined in a different proportion will give hydrogen peroxide, with quite other properties.

A "character" now emerges as the clear-sighted have always seen it—a resultant of a large number of inner agencies, interacting with a large number of outer agencies. The term "unit character" should never have been used, although "unit character-difference" might be permissible.

The great advances of the genetics in the immediate future are thus likely to be in the border area between developmental physiology and genetics in the narrow sense. In this field, the greatest advances have been made outside America, notably by Goldschmidt with his far-reaching work on the genetics and developmental physiology of intersexuality, and Haecker with his "Phänogenetik." *Drosophila* is an unsuitable animal for such studies, owing to its complete metamorphosis and its featureless and inaccessible larva. For this reason, small fish, Crustacea, paurometabolous insects and those whose larvae have abundance of structural features, are likely soon to usurp the centre of the genetic stage. Experiment will become more laborious, since each factor will have to be examined not for a single final effect, but for the type and rate of change which it produces; and physiology will be able to join hands with pure genetics.

How important such studies are likely to become may be indicated by a couple of examples. Schultz showed that the albino parts of the fur in the Himalayan rabbit and even in some true albinos were not white because of a total absence of some colour-producing gene, but because the threshold for pigment-production could not normally be reached there. If part of the skin be shaved and the animal exposed to cold, the new hairs contain pigment. The normal pigmentation of ears, muzzle, etc. in the Himalayan, is thus apparently an indication, not of a segregation of factors during development, but of a lower temperature in such exposed areas. Again, Ford and myself, working with *Gammarus*, have found that there exist different factors for the deposition of black pigment in the red eye at different rates. The slower the deposition, the later it begins. The deposition caused by one gene only begins after sexual maturity; thus if *Gammarus* were a holometabolous insect, it is probable that this factor would never be able to show any effect! One may also hazard the suggestion that multiple allelomorphs series exert their characteristically graded effects owing mainly to differences in their rates of action.

This review of progress is in large measure a review of Morgan's book: but we may now turn more specifically to its contents and his modes of treatment. In a brief but pithy opening paragraph he stresses the fact, forgotten by some and denied by others (generally those who have not taken the trouble to digest the evidence) that the theory of the gene differs from all other particulate theories of heredity in that previous theories in-

vented speculative units to which any properties could be attached, whereas, in this case, the facts came first, and the very existence of gene-units had to be postulated to fit the data of quantitative experiment.

A straightforward presentment of the laws of Mendel and of linkage is followed by a discussion of their chromosomal basis, with a frank admission that genetics has outrun cytology as regards crossing over (in precisely the same way, it might be pointed out, as cytology at one time outran genetics in regard to sex-determination). An admirable résumé follows of chromosome aberrations in *Drosophila*, which is succeeded later in the book by a whole series of chapters on similar phenomena (including polyploidy) in other organisms. I would draw attention especially to the discussion on *Datura*, on *Oenothera* and on Mosses.

The bulk of the rest of the book is taken up with an account of the determination of sex and the physiology of its development. Chapters on the origin and nature of mutations, an excellent but too brief discussion of species-crosses, a section on gene-stability and some general conclusions complete the volume. The important recent results of botanists in obtaining fertile and stable new forms by crossing distinct species should be studied by every biologist interested in systematics or in evolution.

One or two criticisms may be made. The section on Lamarckism should either have been omitted or else made considerably more exhaustive. As it is, there is no mention in it of the work of Guyer and Smith with rabbits, of Metalnikoff on caterpillars, of Jollos on *Paramecium*, or of Harrison on melanic moths.

In the chapter on sex, the statement concerning Goldschmidt's theory of the origin of intersexuality in *Lymantria* seems to me somewhat unfair. As is well known, Goldschmidt postulates that a "female intersex" is one which starts existence as a female, but later becomes male, and vice versa: that the precise moment at which the change of sex occurs depends upon the relative "potency" of male-determining and female-determining factors, which in its turn would determine the time at which the effects of one would catch up with those of the other.

Morgan says that this view is bound up with "assumptions concerning enzymes that are philosophical rather than chemical;" and that Goldschmidt's basal assumption, namely that whichever enzyme starts first, is overtaken later by the other, is not a normal feature of enzyme behaviour.

With regard to the latter point, Goldschmidt's "basal assumption" is hardly that ascribed to him by Morgan, but is to the effect that the rate of production of male and female-determining substances is proportional to the potency of the sex-factors.

Quite apart from any such assumptions, however, Goldschmidt's *general* conclusions are as securely based on fact as were Mendel's. It does seem to be definitely a fact that the *Lymantria* intersexes do start life of one sex, and change to the other; that the moment of sex-change varies; and that the precise moment depends upon the balance of two hereditary factors or sets of factors (of which the male-determining is certainly borne in the X chromosome), which can be combined to give whatever results the experimenter chooses. Goldschmidt has, it is true, confused the issue by advancing a number of subsidiary hypotheses which are either unnecessary or even misleading: but this should not detract from his fundamental achievement. This fundamental achievement, as it appears to me, is the correla-

tion of differences between genes with differences between rates of developmental processes.

The Morgan school have practically completed the essentials of what Mendel initiated—a static theory of heredity, concerning the existence and distributions of genetic units. Goldschmidt has here initiated a dynamic view, concerning the relation of genetic units to development, and I venture to say that as time passes we shall come to look on his work as fundamental for this branch of genetic science.

Morgan himself tells us (p. 26) that "the theory of the gene as here formulated, states nothing as to the way in which the genes are connected with the end-product or character," but adds that knowledge of the way in which the genes produce their effects would, no doubt, greatly broaden our ideas relating to heredity and probably make clearer many phenomena that are obscure at present.

It is the more to be regretted that later (p. 32) he speaks of the chromosomes and their behaviour as going "far toward furnishing a mechanism of heredity" when what is really meant is a mechanism for the distribution of hereditary factors. The mechanism of heredity is developmental as well as distributional; and today, more than ever, this needs to be emphasized.

Finally it remains to touch on the evolutionary bearings of the theory of the gene as here set forth. It remains an undoubted fact, which Morgan frankly admits, that the majority of recorded mutations in *Drosophila* and elsewhere are deleterious in their effects. The opponents of Mendelism, of course, seize on this fact and deny all evolutionary significance to mutations, which they dismiss with the epithet "pathological."

Morgan rightly stresses the fact that the majority of mutations studied by the geneticist are chosen by him because of their striking nature, and that it is likely that striking mutations of large extent will frequently be deleterious; equally rightly he stresses the fact that many small character-differences, often of physiological or biological value have been shown to depend upon inherited unit-factors.

In spite of this there does seem to remain a very real difficulty. In the first place, we are now in a position to assume that every character-difference inherited according to Mendelian principles depends upon a difference between genes in the chromosomes. But we are not yet in a position to assert that all gene-differences owe their *origin* to similar causes. Because white eye in *Drosophila* owes its origin to a single-factor mutation is no reason for supposing necessarily that a Mendelian size-difference found to exist between two races of corn originated in the same way. If Harrison's important work on the induction of melanism in Lepidoptera is confirmed, single-gene mutations may sometimes be induced by specific treatments, as well as originating in an apparently spontaneous way.

We should expect every specific alteration to a chromosomal unit to be inherited in Mendelian fashion: but the alteration might well be brought about in a dozen different ways. Thus in its present condition, the theory of the gene is only knocking at the door of evolutionary theory. Over and over again it demands to be taken into serious account; but it has not yet achieved all that was at one time hoped for from it on the constructive side.

There remains to be mentioned the puzzling but important work of Sumner and his associates on the results of crossing subspecies and local races of mice. The results do not, at first sight, conform with

Mendelian expectation. It is much to be hoped that more work of this nature will be done on natural races. Meanwhile, again, the incompleteness of our evolutionary theory is revealed. One positive point is interesting. Neo-Mendelism is coming round to lay greater and greater stress upon the evolutionary importance of small variations, thereby coming into agreement with systematic zoology and paleontology. It may be that with further analysis the antinomy between "mutation" and "continuous variation" will be shown to have rested on utterly false bases!

Meanwhile, apart from all such bearings, developmental and evolutionary, Neo-Mendelism has provided biology with a vast body of important facts and with tested theories of fundamental importance, and has been the method of familiarizing biologists with the necessity for rigorous, quantitative experiment. It is an achievement to be proud of: and its main lines are ably and interestingly set forth in Morgan's lucid book.

BRIEF NOTICES

EVOLUTION

THE MECHANISM AND MEANING OF LIFE. *Showing How Death Is Humanity's Crime Against the Individual, and Involving Evolution and the Immaculate Conception.*
By Granville Gates with the collaboration of Anne Williams Gates.
Frederick H. Hitchcock
$1.50 5 x 7½; 59 *New York*

The essence of this contribution to The Higher Spiritual Biometry seems to be that "the man who fell by assuming two motives unequal in effect divided himself by two in 'spirit,' actinic power, 'will,' thought or mental action (man and woman); by three in 'mind,' decision, dynamic power or physical action (man, woman and child) and by four in 'body,' static power, potential or physical result (man, woman, child and humanity). Thus humanity is Fallen Man as a mental-physical whole whose past is woman or unconscious or physical diversity of 'sex' and whose future is in the perfection of child or the mental or conscious uniting of 'sex.'

"The following therefore seems to express the full 'sex' or family relation:

Woman = 0.222 (Mental) (Individual woman)
Child = 0.111 (Physical) (Individual man)
Imperfect Man = 0.333 (Mental) (Collective man)
Humanity = 0.666 (Physical) (Collective woman)

•Fallen Man as a Whole = 0.999 (Mental-physical)

"Humanity is therefore the predominating and relatively inert constant ('666') which retards the reversion of its individuals to instantaneous functional equality." (P. 30.)

From these data the following somewhat startling conclusion is reached: "The period of a woman's true maturity from 22.2 to 33.3 years may be said to be the perfectly voluntary or Christ child period. *In this period the immaculate conception should be relatively easy physically and fairly easy mentally.*" (P. 33.) (Our italics.)

THE GIST OF EVOLUTION.
By Horatio H. Newman. The Macmillan Co.
$1.50 5¼ x 7¾; ix + 154 *New York*

A tract of the times engendered by the Scopes trial at Dayton, Tennessee. Chapter III to XII (the end of the book) deal

with purely biological matters and furnish an excellent, brief, popular review of our present knowledge of organic evolution. The first two chapters devote themselves to philosophy and theology, with less happy results. We think that some of our more philosophically minded readers may be entertained by the following quotation (see page 20): "It is deeply to be regretted that the enemies of science have tried to convince their hearers that science and religion are irreconcilable. This cannot be true, for not only are many men of science genuinely religious, but many theologians and great Christian leaders are in entire accord with the scientific views of the time." And still we hear animadversions on the depth of the philosophy and the precision of the logic of fundamentalists!

GENETICS

Vacant

GENERAL BIOLOGY

THE NEW NATURAL HISTORY. *Volume I.*
By J. Arthur Thomson. G. P. Putnam's Sons
$6.00 8 x 10½; 388 *New York*

Perhaps there is a subtle and recondite plan behind the arrangement of the material in the first volume of this magnificent, new, popular natural history, but if so it has been concealed with uncanny skill. The reader *seems* to be led about in an entirely casual and haphazard fashion among the wonders of animate nature. The very casualness of the sudden transitions from gorillas to ants, or from squids to spiders, undoubtedly adds to the charm of the book for the general reader. In his foreword Professor Thomson states that he has been led in this work "to treat of animals not only as threads in a quivering web of life, but as personalities of a sort, which seek after well-being, which even share in their own further evolution. And in this last word the keynote of our New Natural History is sounded, for, without formal discussion of difficult questions, we have sought to illustrate the biggest fact of all, that Animate Nature is a drama still going on." As was to be expected from the author's past performances, the book is charmingly written and beautifully illustrated, mostly from photographs. Altogether the book is an achievement. It should certainly be in every home where there are children. We know of no book on natural history half so thrillingly interesting or so casually unsystematic in its arrangement.

PATHOGENESIS.
By Carl F. Jickeli. R. Friedländer und Sohn
15 marks 6½ x 10; xv + 335 (paper) *Berlin*

A philosophical contribution to theoretical biology by a man who has never been a professor, but instead appears to have spent his life in the practice of medicine in a small town far from scientific centers. Whether there is any causal connection or not, there certainly seems to be a correlational association between this fact and a certain freshness and novelty in his discussion. The main tenets of the author's faith are two concepts; one of the incompleteness of metabolism, and the other of a principle of organic stability. Starting from these bases he synthesizes a general philosophy of all biological phenomena, but pays especial attention to the origin of disease. The book seems to be of no great importance, but contains a number of ideas of

real interest and originality. The author's knowledge of the literature of general biology is extensive, but spotty.

DIE GESCHICHTE DER BIOLOGIE. *Ein Überblick.*
By Erik Nordenskiöld. *Gustav Fischer*
25 marks 6¼ x 9⅝; vii + 648 (paper) *Jena.*

There has long been a need for a comprehensive and systematic history of biology, handled from a modern point of view. This book, which is a German translation of a series of lectures given at the University of Helsingfors in 1916 and 1917, and subsequently published in Swedish, comes nearer to filling this need than any book which has yet appeared. The material is treated in five main divisions: Biology in the classical period and in the Middle Ages; biology during the Renaissance; biology in the seventeenth and eighteenth centuries; biology in the first half of the nineteenth century; development from Darwin to the present time. There is a section on sources and literature and a detailed index. The book would have been improved by illustrations, but as it stands it is a worthy and welcome addition to the literature of the history of science.

JUNGLE ISLAND.
By Warder C. Allee and Marjorie Hill Allee.
Rand McNally and Co.
$1.00 5 x 7¼; x + 215 *Chicago*

"Jungle Island" is Barro Colorado Island in Gatun Lake, in the Panama Canal Zone. This book is intended for children. It may be characterized as a series of more or less entertaining tales about various aspects of tropical nature. It is extensively but unevenly illustrated. The line diagrams are in the main satisfactory, but some of the photographs are so badly reproduced as to appear merely as black smudges on the page. This seems a great pity, because obviously in many cases the original photographs were excellent. There is a short chapter of suggestions to teachers and a glossary, from which the inquisitive infant may learn that the technical term "buoy" means "A float marking safe channels for ships," and that "fumigate" is "To smoke out bacteria, insects, or large animals." It seems a little unfortunate to have dragged bacteria into this latter definition.

AVORTEMENT ET STÉRILITÉ.
By H. Vignes et G. Barbaro, P. Rinjard, E. Curot and J. Dufrénoy.
Revue de Pathologie Comparée et d'Hygiène Générale
8 francs 6½ x 10; 110 (paper) *Paris*

This volume reprints four papers presented at a meeting of the Society of Comparative Pathology of Paris on November 10, 1925. The first paper, by H. Vignes and G. Barbaro, discusses the causes and mechanisms of abortion in the human species; the second, by P. Rinjard, deals with the contagious abortion of cattle (Bang's disease); the third, by Ed. Curot, is on the pathogenesis and diagnosis of sterility in domestic animals; the final paper, by J. Dufrénoy, is on sterility in plants. The first paper is the best in the volume, and the last the worst. Apparently M. Dufrénoy has never heard of the brilliant and fundamental work of East on sterility in plants.

LA MORT ET LA BIOLOGIE. *Essais sur la Mort.*
By Henry de Varigny. *Félix Alcan*
12 francs 4¾ x 7½; 309 (paper) *Paris*

A rather comprehensive review of existing knowledge and opinion about the biology of death, life duration, and senescence. Its authorship by the veteran French biologist, Henry de Varigny, insures, on the one hand, its general accuracy as to facts, and, on the other hand, its literary charm, for there are few writers of science for the people anywhere in the world whose literary gift equals that of de Varigny. The book falls in two parts, the first dealing with the various aspects of senescence and death in the lower organisms, and the second with death in the human species. It is an interesting little treatise.

GOETHE'S NATURWISSENSCHAFTLICHESCHRIFTEN. *Band I and Band II*
Insel-Verlag
28 marks *Leipzig*
Band I, 885
4¼ x 7; Band II, 698, 31 pp. figures

In these two attractive little volumes, printed on India paper, the major portion of Goethe's writings on natural science are reprinted. The first volume falls into three main divisions—an opening general section, followed by the papers on biology, which are again followed by those on geology. The second volume deals with Goethe's theory of color and color vision.

THE BACTERIOPHAGE AND ITS BEHAVIOR
By F. d'Herelle (Translated by George H. Smith). *The Williams & Wilkins Co.*
$8.00 6 x 9; xiv + 629 *Baltimore*

This detailed technical account of the development of the present understanding of the bacteriophage, by its distinguished discoverer, is a welcome addition to the literature of general biology and immunology. The book is divided into three principal parts dealing respectively with the following subjects: The phenomenon of bacteriophagy; The bacteriophage; The behavior of the bacteriophage protobe. There is a bibliography of 647 titles, and detailed author and subject indices. Altogether is an achievement of which the author, the translator, and the publisher may all well be proud.

DAS INDIVIDUALITÄTSPROBLEM UND DIE SUBORDINATION DER ORGANE. (*Ein Beitrag zum Descensus der Keimdrüsen der Säugetiere.*)
By Dr. Armin Müller.
Akademische Verlagsgesellschaft M.B.H.
Marks 3.50 6 x 9; 95 (paper) *Leipzig*

A highly abstruse contribution to the philosophy of biology. The descent of the mammalian testes and the organization of the central nervous system are taken as examples illustrative of the author's theory of organic pattern and integration.

JOHANNES MÜLLER. *Das Leben des Rheinischen Naturforschers.*
By Wilhelm Haberling.
Akademische Verlagsgesellschaft M.B.H.
22 marks 6½ x 9½; 501 (paper) *Leipzig*

A well arranged and well written biography of a great man, which includes a considerable amount of new material, especially an extensive selection from his letters. It is a valuable addition to the history of science.

HUMAN BIOLOGY

THE NEED FOR EUGENIC REFORM
By Major Leonard Darwin. *John Murray*
12 shillings 5½ x 8½; xvii + 529 *London*

This is the most extensive treatise on eugenics, intended for the general reader, that has yet appeared. The distinguished author is the son of Charles Darwin, to whose memory this volume is dedicated, and has been for thirteen years the leader of the eugenics movement in England on its popular side, having held during this period the presidency of the Eugenics Education Society, founded by Galton. While the material itself is largely based upon Major Darwin's lectures and addresses in this field, it is not merely a reprint but the whole has been reworked into coherent and unified form. The twenty-seven chapters range over the whole field of topics that have been discussed by eugenists since the movement was started. As is to be expected, a great deal more space and emphasis is devoted to the negative than to the positive side of the subject. In the present state of knowledge it is much easier to write about race deterioration than it is to tell how to establish in the race desirable qualities. Not all biologists or sociologists or economists will agree with all the positions taken by the author in regard to the many controverted points which are always necessarily to the fore in eugenic discussions, but at the same time specialists in each one of these fields, as well as the general reader for whom the book is intended, will find much in it to stimulate and inform his thought. The book is well indexed.

THE WORSHIP OF NATURE. *Vol. I*
By Sir James George Frazer.
The Macmillan Company
$4.00 6 x 8½; xxvi + 672 *New York*

This treatise by the distinguished author of "The Golden Bough" displays again his immense and profound learning. The book originated as a series of Gifford Lectures on natural theology at the University of Edinburgh in 1924 and 1925, but in its printed form considerable additional material has been included. The book describes in great detail the manner in which primitive peoples came to personify and worship the Sky, the Earth, and the Sun, as deities capable of influencing human life. The extent and manner of development of this tendency, as well as its social effect, are described for the ancient Aryans (the Vedic Indians, old Persians, Greeks, and Romans). There next follow similar accounts for the ancient Babylonians, Assyrians and Egyptians, the Chinese and Indo-Chinese, and existing primitive races in different parts of the world—India, America, etc. The sources in the literature are extensively and minutely documented. The book is a contribution of first rate importance to cultural anthropology.

MONGREL VIRGINIANS. *The Win Tribe.*
By Arthur H. Estabrook and Ivan E. McDougle. *The Williams & Wilkins Co.*
$3.00 5 x 7½; 205 *Baltimore*

In the making of this detailed study of a family group in the Virginia mountains a geneticist and a sociologist have collaborated, with distinctly good results. The Win family tribe is made up of morally and intellectually low grade people, who represent a combination of three divergent racial stocks—white, Indian, and negro. In part at least as a result of social ostracism, there has been much inbreeding in the tribe. The study has been made with great critical care and constitutes a valuable addition to the literature of eugenics. It is particularly unfortunate that a book

of this type, of which a major part is filled with detailed family records, has no index.

KÖRPERMASZE UND KÖRPERPROPORTIONEN DER ISLÄNDER. *Ein Beitrag zur Anthropologie Islands.*
By Gudmundur Hannesson.

Fjelagsprentsmidjan
$2.50 *Reykjavik, Iceland*
$6\frac{5}{8}$ x $10\frac{1}{2}$; vii + 254

This is a contribution to the original literature of anthropology of first-rate importance. The author has measured over a thousand male Icelanders of various ages. In addition to the detailed biometric treatment of his measurements, the author reviews all that is known regarding the anthropology of Iceland. He finds the Icelandic race to be predominantly Nordic; tall, slender statures predominate, with comparatively long faces and light eyes. The variability in respect of types is nevertheless great. Short stature, combined with square build, is common. Mixed or dark eyes are not uncommon. He concludes that besides the Nordic, the Alpine race, and probably the Baltic race too, are to be found in Iceland, and very likely also the Mediterranean race, the last having been imported with the colonists from Scotland and Ireland. There is an adequate bibliography, but, unfortunately, no index.

LES VARIATIONS DU CORPS HUMAIN.
By L. Dubreuil-Chambardel.

Ernest Flammarion
10 francs $4\frac{3}{4}$ x $7\frac{1}{4}$; 250 (paper) *Paris*

This interesting treatise by the President of the Anthropological Society of Paris discusses in a semi-popular, but authoritative manner, some of the more outstanding facts of human teratology, and to a lesser extent those concerning the normal variations of the human body. The main divisions of the treatment are as follows: The general variations of the body (including such matters as dwarfism, gigantism, etc.); the variations of the trunk; the variations of the head; the variations of the hands and feet; congenital absence of the limbs; variations in the genital organs; variations of the skin. The book is rather fully illustrated in an interesting way but, unfortunately, the reproduction of the illustrations is inadequate.

POPULATION PROBLEMS IN THE UNITED STATES AND CANADA. *An Outgrowth of Papers Presented at the Eighty-Sixth Annual Meeting of the American Statistical Association, December, 1924. (Publications of the Pollak Foundation for Economic Research No. 5)*
Edited by Louis I. Dublin.

Houghton Mifflin Co.
$4.00 $5\frac{1}{4}$ x 8; xi + 318 *Boston*

In this volume, made up of contributions by some twenty odd writers, various phases of population growth, and its connection with natural resources, immigration, and the labor supply, are discussed. As is to be expected in such a work, the contributions are of varying degrees of merit. The papers by Dr. Warren S. Thompson on the natural increase of population, by Prof. Don D. Lescohier on population and agriculture, and by Dr. Aleš Hrdlička on the effects of immigration on the American type, are particularly worthy of mention. Taken as a whole the book is a timely reference work on the population problem. It is attractively printed and well indexed.

EUGENICS AND POLITICS.
By Ferdinand Canning Scott Schiller.
Constable and Co., Ltd.
8 s. 6 d. 5¾ x 8¾; xi + 220 *London*

This volume by the brilliant Oxford philosopher reprints a series of essays which he has at various times contributed to journals, principally the *Eugenics Review*. The most entertaining essay in the volume is the fifth, "Plato and Eugenics," which is also the oldest, having been written in 1899. Altogether the volume is a contribution to the lighter literature of eugenics worthy to rank with the writings of Sir Francis Galton himself in the same vein. This is saying a good deal, because in many quarters the propaganda for eugenics has sadly deteriorated in its quality since Galton's death.

DER DILUVIALE MENSCH IN EUROPA.
By Dr. F. Birkner. Verlagsanstalt Tyrolia
Rm. 5.30 5¾ x 8¼; 148 (paper) *Innsbruck*

Considering its small size, and therefore necessary omission of all details, this is one of the best accounts of the present knowledge of prehistoric man that has come to our attention. There are 278 illustrations, well reproduced. The material is presented under four main heads, as follows: The material culture of prehistoric man; the culture of prehistoric man in Central Europe; the psychological characteristics of prehistoric man; his structural characteristics. The book closes with a short, but well chosen, bibliography.

A HISTORY OF AGRICULTURE IN EUROPE AND AMERICA.
By Norman S. B. Gras. F. S. Crofts and Co.
$3.50 5¾ x 8¾; xxvii + 444 *New York*

A text-book which not only sets forth in considerable detail the historical facts in regard to agriculture and rural social and economic life in general, but also makes some attempt to elucidate the meaning of these facts in relation to human evolution. It is extensively documented with bibliographic material, contains a detailed index, and is well arranged for teaching purposes. The author is professor of economic history in the University of Minnesota.

LA FAMILLE SYPHILITIQUE ET LA FAMILLE CANCÉREUSE.
By Dr. Pfeiffer (de Dijon). Norbert Maloine
1 franc 6 x 9; 22 (paper) *Paris*

This pamphlet maintains the strange thesis that syphilis is the clinical cause of cancer. The author has studied sixty-six families in which cancer has occurred, and holds that it is always accompanied either by the stigmata of hereditary syphilis or the clinical signs of acquired syphilis. The evidence falls something short of completely proving the thesis.

ZOOLOGY

THE ARCTURUS ADVENTURE. *An Account of the New York Zoological Society's First Oceanographic Expedition.*
By William Beebe. G. P. Putnam's Sons
$6.00 6½ x 9½; xix + 439 *New York*

The author of this book is able to combine business and pleasure more skillfully and successfully than any other scientific man ever known. In reading this gorgeously illustrated and beautifully printed volume there is an intensive impression of Beebe's unfailing joyousness in his work. His attitude towards his science is extraordinarily like that of Benvenuto Cellini towards his art. This

book is easily the best of the author's popular writings. It is essentially a layman's log of the expedition of the Arcturus, lavishly outfitted for a general zoological and oceanographic *reconnaissance* in American tropical waters. Whatever scientific results the expedition may have achieved will be separately reported in other publications. In this volume are presented many observations of animal behavior, particularly that of the entertaining mammal, William Beebe.

ANIMAL ECOLOGY.
By A. S. Pearse. *McGraw-Hill Book Co.*
$4.00 6 x 9; ix + 417 *New York*

There has been for some time a need for a systematic treatise on animal ecology. This work has been written to fill this need. After an introductory chapter largely concerned with definitions, the following topics are discussed: Physical and chemical ecological factors; biological factors; succession; animals of the ocean; freshwater animals; terrestrial animals; the relations of animals to plants; the relations of animals to color; intraspecific relations; interspecific relations; the economic relations of ecology. There is an extensive bibliography, arranged alphabetically by authors, covering some thirty pages. Curiously enough, the book contains no illustrations. We believe it to be unique among treatises on ecology in this respect. It is a well written and useful addition to the literature, without being in any sense profound, or particularly original.

BRITISH BIRDS. (*Volume III*)
By Archibald Thorburn.
Longmans, Green and Co.
$5.50 6 x 9; x + 169 *New York*

The first two volumes of this important work have already been noticed in earlier numbers of *The Quarterly Review of Biology*. The third maintains, and perhaps even surpasses, the high standard of quality set in the other two. Perhaps one reason why the plates seem more beautiful in this volume than in others is that the ducks, pheasants and grouse lend themselves particularly to artistic ends. The 48 plates in this volume illustrate birds belonging to the following orders: *Herodiones*, *Anseres*, *Columbae*, *Pterocletes*, *Gallinae*, *Grallae*, *sub-order Fulicariae*, *sub-order Otides*, and *Limicolae*. The reproductions of Mr. Thorburn's wonderful paintings are superb. He attributes the marked increase in ducks nesting in Britain to better protection through recent game laws. We wonder just how great a part this particular element in the total ecological situation has really played in producing the observed result.

DIE TIERWELT DER NORD- UND OSTSEE. (*Lieferung I, II and III*)
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft M. B. H.
Lieferung I, 4.80 marks *Leipzig*
6 x 8½; 79 (paper)
Lieferung II, 4.50 marks
6 x 8½; 72 (paper)
Lieferung III, 7.80 marks
6 x 8½; 100 (paper)

The aim of this new series is to give a comprehensive, fully illustrated account of the fauna of the North Sea and the Baltic, with particular attention to the ecology and biology of the animals living in these waters. It is expected that the work will be completed in about three years and will include, all told, about 120 signatures. The first three parts now at hand deal with the following groups: *Opisthobranchia* and *Pteropoda* by H. Hoff-

man; *Scaphopoda* by T. van Benthem Jutting; *Amphibia* and *Reptilia* by R. Mertens; *Noctiluca* by A. Pratje; *Teleostei Physoclisti* and *Heterosomata* by W. Schnakenbeck; *Echiuridae*, *Sipunculidae*, *Priapulidae* by W. Fischer; *Enteropneusta* by C. J. van der Horst; *Pantopoda* by J. Meisenheimer. The illustrations are line cuts in the text and are in the main diagrammatic. So far as may be judged from the present parts the work will be, when completed, a useful reference source.

BATTLES WITH GIANT FISH.
By F. A. Mitchell-Hedges.
Small Maynard Company
$5.00 6 x 9; 300 *Boston*

A most entertaining account of the author's adventures during two years of fishing in the Caribbean Sea and the Pacific Ocean. It is abundantly and rather thrillingly illustrated with photographs taken by Lady Richmond Brown, who accompanied the author on his expedition. Throughout the book there is an obvious effort to impregnate the tale with a flavor of scientific research, but actually the only records of any permanent value are of the enormous sizes to which some fish may attain, particularly the cartilaginous fishes (sharks, rays, etc.). There is no need, however, for the reader to be inhibited by any consideration of this book as a scientific treatise. If he will simply regard it as a tale of adventure he will be rewarded by excellent entertainment and some real thrills.

ZOOLOGISCHES WÖRTERBUCH.
By Dr. Erwin Hirsch-Schweigger.
Walter de Gruyter and Co.
26 R. M. $5\frac{1}{4}$ x $7\frac{1}{2}$; viii + 628 *Berlin*

This well illustrated zoological dictionary will be found a valuable addition to any library. The system of cross-referencing is extremely well conceived and carried out to a fineness of detail that we know of in no other technical dictionary. Pronunciations of technical names are indicated by the use of accents. American readers will find some of these indicated pronunciations different from the accustomed usage here. But this is a trivial defect. Altogether we recommend this dictionary highly, especially to high school and college departments with meager library facilities. It is a pity that there is no such work in English.

THE BOOK OF THE RED DEER.
Edited by John Ross.
Simpkin, Marshall, Hamilton, Kent and Co., Ltd.
10 s. 6 d. $8\frac{1}{4}$ x $10\frac{1}{4}$; 161 *London*

This is an entertaining, well produced contribution to the literature of big game hunting. There are twelve chapters contributed by as many different writers. The major portion of the book is devoted to the red deer of Scotland. While written in a popular vein, mammalogists will find a good deal in it of interest. An appendix contains a detailed list of all the deer forests in Scotland, with statements as to area, ownership, etc.

EMPIRE BIG GAME.
Edited by Hugh Gunn.
Simpkin, Marshall, Hamilton, Kent and Co., Ltd.
10 s. 6 d. $8\frac{1}{4}$ x $10\frac{1}{4}$; 228 *London*

This is a companion volume to the one reviewed immediately above, constructed on the same plan, and carrying in some part the same material. Primarily, however, this volume is devoted to the big

game of the outlying parts of the British Empire, including Canada, Newfoundland, Australia, Africa, India, and Malaysia. These are contributed by different authorities on the hunting and wild life of these regions. Both volumes are illustrated with excellent photographs, and may well find a place on the shelves of any library of natural history.

AN ACCOUNT OF THE CRUSTACEA OF NORWAY. *With Short Descriptions and Figures of all the Species. Volumes VIII and IX.*

By G. O. Sars.

Published by The Bergen Museum, Bergen; sold by Alb. Cammermeyers Forlag, Christiania

Vol. VIII, Kr. 15,00;
8 x 11½; 91 (paper)

Vol. IX, Parts 1–12, Kr. 30,00
8 x 11½; 176 (paper)

In Volume VIII of the author's great work on the crustacea of Norway the *Monstrilloida* and *Notodelphyoida* are set up as distinct divisions of the *Copepoda*, and the following families are placed under them and described: *Thaumatopsyllidae, Monstrillidae, Notodelphyidae, Doropygidae, Buproridae, Ascidicolidae, Botryllophilidae, Enterocolidae.*

Volume IX begins an account of the *Ostracoda*, and in the parts so far issued the following families are discussed: *Cypridinidae, Conchoeciidae, Polycopidae, Cytherellidae, Cypridae, Cytheridae.*

MEMÓRIAS DO INSTITUTO DE BUTANTAN. 1925. *Tome II—Fasciculo Unico. Contribution à l'étude du venin des araignées, par les Drs. Vital Brazil et J. Vellard. Un nouveau genre et deux espèces nouvelles d'araignées de l'état de S. Paulo, par le Dr. J. Vellard. Immunisation antitétanique par la méthode toxoide-toxine, par le Dr. J. Lemos Monteiro. Les différentes phases de l'autolyse du "B. anthracis," par le Dr. J. Lemos Monteiro. Immunisation per os contre le bacille de Shiga. Contribution à l'étude du mécanisme de l'immunité, par le Dr. Eduardo Vaz.*

Instituto de Butantan
7 x 10; 119 (paper)
São Paulo, Brazil

The chief general biological interest of this volume lies in the first two memoirs which take up about three-quarters of the space. They deal with the poisonous spiders of Brazil and their venom in a thorough-going, systematic manner. The volume is a welcome addition to the reference shelves of any zoological library.

NOTE D'ORNITHOLOGIE. *Remarques et Observations sur l'Habitat, les Moeurs, la Migration, etc., de la Bécassine Double (Gallinago media Frisch, 1763).*

By Paul Petitclerc. *Éditions Bossard*
45 francs *Paris*
7¼ x 9½; 89 + 3 plates (paper)

A monographic account of the solitary or double snipe, illustrated with three fine photogravure plates. After a description of the external morphology of the bird, such matters as habits, flight, migration and local distribution are discussed in detail. Finally, to round out this excellent monograph, a section is devoted to the culinary importance of the double snipe, clearly indicating that the author is a gentleman as well as a scholar.

DIE HAUSINSEKTEN UND IHRE BEKÄMPFUNG.

By Max Dingler. *Paul Parey*
Rm. 2 5 x 7½; 96 (paper) *Berlin*

This little popular treatise on insect

pests of the household, and methods of controlling them, is of precisely the same character as the practical bulletins which the United States Department of Agriculture distributes free to residents of this country.

MANIPULATIONS ZOOLOGIQUES
A l'usage du P. C. N., des Écoles Normales et des Candidats au Brevet supérieur et au Professorat des Écoles Normales.
By Léon Bertin and Amélie Boisselier.
Les Presses Universitaires de France
20 francs $7\frac{1}{4}$ x $9\frac{1}{4}$; x + 335 (paper) *Paris*

A laboratory manual for a course in zoölogy, roughly corresponding in content and depth to the zoological part of American college courses in general biology plus vertebrate comparative anatomy. It is extensively illustrated, chiefly with schematic diagrams. There is a detailed glossary of technical terms.

DISEASES OF DOMESTICATED BIRDS.
By Archibald R. Ward and Bernard A. Gallagher. *The Macmillan Co.*
$3.25 $6\frac{1}{4}$ x $9\frac{1}{4}$; xii + 333 *New York*

A practical treatise on poultry pathology, developed along conventional lines, but bringing into the account of each disease the results and observations reported in recent literature. The book is fairly well illustrated and has author and subject indices.

PALAEONTOLOGY. *Invertebrate.*
By Henry Woods. *The Macmillan Co.*
$3.50 5 x $7\frac{1}{4}$; 424 *New York*

This is the sixth edition of the well-known introduction to invertebrate palaeontology, first published in 1893. There is a good bibliography and a detailed index.

BOTANY

THE NERVOUS MECHANISM OF PLANTS.
By Sir Jagadis Chunder Bose.
Longmans, Green and Co.
$6.40 $5\frac{3}{4}$ x 9; xix + 224 *New York*

If accepted at its face value, the evidence in this volume would be sufficient to establish the author's thesis that there is present in plants a tissue which corresponds in its physiological behavior to the nervous tissue of animals. Just as in his numerous former researches the distinguished Indian botanist, Sir Jagadis Chunder Bose, has brought to the study of the problems dealt with in the present volume rather elaborate and highly sensitive pieces of apparatus of his own devising. The general conclusions reached are as follows: "It can no longer be doubted that plants, at any rate vascular plants, possess a well-defined nervous system.

"It has been demonstrated that excitation is conducted by the phloem of the vascular bundle, and that conduction in this tissue can be modified experimentally by the same means as is that in animal nerve. The conducted excitation may, therefore, be justly spoken of as nervous impulse and the conducting tissue as nerve.

"It has been further shown that, as in the animal, it is possible to distinguish sensory or afferent and motor or efferent impulses, and to trace the transformation of the one into the other in a reflex arc. The observations involve the conception of some kind of nerve-centre. No structure corresponding to the nerve-ganglion of an animal has, indeed, been discovered in the pulvinus of *Mimosa pudica*, but it is not impossible that the physiological facts may one day receive histological verification."

The difficulty, of course, is that neither plant physiologists nor animal physiologists are as yet inclined to accept Professor Bose's evidence quite at its face value. But the fact that the matters discussed are still under judgment, and the subject of controversy, in no wise detracts from the interest and value of this well written book, as a document of record.

KURZES LEHRBUCH DER ALLGEMEINEN BAKTERIENKUNDE.

By Rudolf Lieske. *Gebrüder Borntraeger* G. M. 15 *Berlin*

6½ x 10; viii + 338 (paper)

This is a valuable and interesting contribution to the literature of general biology. As the author points out, bacteriology began as one of the special fields of botany. But as soon as it was learned that bacteria were the causes of various diseases of plants, animals, and men the practical importance of this discovery led at once to the development of highly specialized subdivisions of the science of bacteriology, which in their evolution have come at the present time to have little relation to each other. The whole subject of bacteriology is now at the threshold of what will perhaps prove ultimately to have been a radical turning point in its scientific development. New and old points of view stand at the present time in rather sharp contrast. The object of the author in writing this book was to put into the smallest space consistent with clearness and sound treatment, what a student ought to know about the general biology of bacteria before he embarks upon one of the special divisions of bacteriology such as medical, agricultural, or any other. This task, for which there was a real need, has been well done by Doctor Lieske. The topics treated are as follows: Morphology; physiology; enzymes; action of external influences upon bacteria; bacterial symbioses; antagonistic relations between bacteria and higher organisms; the bacteriophage; particular biological groups of bacteria and related organisms; and technical methods of bacteriology. The book is well documented and indexed.

VERGLEICHENDE MORPHOLOGIE DER PILZE.

By Ernst Gäumann. *Gustav Fischer* 28 marks 6¾ x 10⅛; x + 626 (paper) *Jena*

This systematic treatise on the morphology of the fungi by the Botanist of the Swiss Agricultural Experiment Station has as its leading idea to bring the results which have been obtained by bringing modern cytological technique to bear specifically on the taxonomy and comparative morphology of this group. The opening general part of the book contains nothing particularly new, but is an excellent summary of present knowledge of the morphology of the fungi, such as might appropriately find a place in a general text-book of botany. This is followed by a special part in which the different orders are separately discussed in detail. The book is well illustrated, thoroughly documented as to literature, and has a detailed index. Altogether it is a valuable addition to the reference literature of botany, although it is to be regretted that the treatment is so exclusively morphological.

ROOT DEVELOPMENT OF FIELD CROPS.

By John E. Weaver. *McGraw-Hill Book Co.* $3.00 6 x 9; xii + 291 *New York*

This is a detailed and rather technical treatise on a highly specialized and

neglected field of botany, the habits of the roots of plants. Attention is strictly confined to crop plants. In the different agricultural experiment stations a good deal of work has been done in this field, but it has never before been collected together. Approximately the first half of the book is devoted to general topics regarding root development, such as the soil, the morphology of roots, and the behavior of roots of numerous plants. The remainder of the book contains special chapters on different important crop plants. There is a bibliography of 232 titles, and an excellent index.

THE HYDROSTATIC SYSTEM OF TREES. *Carnegie Institution of Washington Publication No. 373.*

By D. T. MacDougal. *Carnegie Institution*
$2.50 *Washington*
$6\frac{7}{8}$ x 10; iii + 125 (paper)

This is a detailed report of the more recent results of the author's extensive investigations on the hydrodynamics of the plant. The experiments here reported were performed on pine, oak, and walnut trees. Three mechanically distinct regions in the trunk are recognized as of fundamental importance in the hydrostatic system of a tree. The first of these is a complete cylindrical shell of living cells in the cambial zone, through which nothing may pass except by diffusion through protoplasm. The second shell is formed by the water column extending, under varying tensions, from the menisci of the transpiring cells in the leaves downward through the recently formed conduits and wood-cells to the root-hair zones in the roots. Finally, in the older central part of the stem, the tracheids contain air and constitute a third component of the system. All of the results of this work are stated to confirm Dixon's conception of the cohesive meshwork column of water as the essential element in the hydrostatic system.

LEHRBUCH DER PFLANZENPHYSIOLOGIE. (*Chemische Physiologie. Band I.*)

By S. Kostytschew. *Julius Springer*
27 reichsmark *Berlin*
$6\frac{1}{2}$ x $9\frac{3}{4}$; vii + 567 (paper)

The first article in the author's creed is that the present day worker in the field of plant physiology must be a trained chemist. In writing this book he has assumed a rather comprehensive knowledge of organic chemistry on the part of the reader. The topics discussed in this first volume are: The bases of chemical plant physiology; the assimilation of the sun's energy by green plants and the primary synthesis of organic substances; chemosynthesis and assimilation of molecular nitrogen; the nourishment of the plant with organic compounds; the nourishment of the plant with ash components and its significance; carbohydrates and proteins and their metabolism in the plant; secondary plant substances; respiration and fermentation.

The book carries rather extensive documentation of the literature and a meager and unsatisfactory index. It will be a useful and important reference book, which one would suppose will ultimately be translated into English.

AN OUTLINE OF PLANT GEOGRAPHY.

By Douglas H. Campbell. *The Macmillan Co.*
$4.00 $5\frac{3}{4}$ x $8\frac{3}{4}$; ix + 392 *New York*

This book is the outcome of the author's

excursions, during more than thirty years past, into many parts of the world in search of material for his botanical studies. It seems to us that the book gains both in charm and in value from the fact that Professor Campbell is not primarily a plant geographer, but has approached this field of botany with a certain spirit of detachment. After an introduction which deals primarily with the succession of plants in geological time, the book discusses the following topics in order: climatic zones; the North Temperate zone; the Palaeotropics; the Neotropical region; the South Temperate zone. The book is well illustrated, many of the photographs being original, and closes with a detailed and adequate index. It is a valuable contribution to botanical literature.

STUDIES ON THE ORIGIN OF CULTIVATED PLANTS.
By N. I. Vavilov.
Institut de Botanique Appliquée et d'Amélioration des Plantes.
—— 7 x 10⅜; 248 (paper) *Leningrad*

This extensive and well illustrated monograph on the origin of cultivated plants by the well-known Russian plant geneticist presents the following topics in detail: Methods of determining the geographical centers of the origin of cultivated plants; geographical centers where the forms of the principal cultivated plants of the Old World have originated; weeds as the progenitors of cultivated plants; mountain districts as the home of agriculture; the origin of primary crops, in particular of cultivated hemp; the ecological principle in the origin of cultivated plants; geographical regularities in the origin of the forms of cultivated plants; the principal world centers of the origin of cultivated plants.

KLIMA UND BODEN IN IHRER WIRKUNG AUF DAS PFLANZENLEBEN.
By Henrik Lundergardh. *Gustav Fischer*
24 marks *Jena*
6½ x 9½; viii + 419 (paper)

This is a systematic textbook of ecology, first developed as a series of lectures in the Masaryk University in Brünn. After a brief historical introduction, the following topics are discussed: The light factor; the temperature factor; the water factor; the formation and general ecological characteristics of the soil; the physical characteristics and aeration of the soil; chemical soil factors; the microörganisms of the soil; the carbon dioxide factor; the guiding principles of experimental ecological investigations. The book is well illustrated and indexed. The author takes throughout the commendable viewpoint that since ecology is a branch of physiology the attitude of physico-chemical precision which has proved so fruitful in laboratory physiology must also be the manner of approach to the problems of ecology.

GEOGRAPHIE DER MOOSE.
By Th. Herzog. *Gustav Fischer*
27 marks *Jena*
6¾ x 10; xi + 439 + 8 plates (paper)

This systematic treatise on the geographical distribution of the mosses, by the Professor of Botany at the University of Jena, is divided into three parts. The first 74 pages deal rather briefly with such general matters as the comparative anatomy of the mosses, and their technical ecological characteristics. In the two remaining parts the known facts about the geographical distribution of these plants are presented successively in two different ways. In Part II the point of departure is taxonomic. The facts about the distribu-

tion of each family, and in less detail each genus and species, are briefly set down. In the third, and final part, the point of departure is the geographic region. For each such region the moss flora is described in detail. There is a bibliography of 633 titles, and detailed indices. The book will be a valuable work of reference.

UNTERSUCHUNGEN ÜBER DIE BEDEUTUNG DER BAUMMYKORRHIZA. *Eine ökologisch-physiologische Studie.*
By Elias Melin. *Gustav Fischer*
7.50 marks 6½ x 9½; vi + 152 (paper) *Jena*

This is a thorough review of our present knowledge of the symbiotic relation between fungi (*Mycorrhiza*) and the roots of certain trees, together with the results of the author's extensive original work on this problem. He has approached the matter experimentally and cultivated separately in pure cultures the root fungi and also the plants, and then in combination pure cultures of the plants and fungi together. It is demonstrated that the *Mycorrhizae* have a vital significance for the plants and trees on certain kinds of soil. There is an excellent bibliography covering six pages.

THE CLASSIFICATION OF FLOWERING PLANTS. *Volume II. Dicotyledons.*
By Alfred B. Rendle. *The Macmillan Co.*
$10.50 5¾ x 8¾; xix + 636 *New York*

This second volume follows the first after an interval of twenty years. It deals with the Dicotyledons. The general arrangement follows that of Engler's *Syllabus der Pflanzenfamilien*. Brief, but adequate, descriptions are given of all the orders and all but a few of the smaller families of Dicotyledons, with frequent illustrations of typical forms. Special emphasis is given to the British flora. There are 279 illustrations and an excellent detailed index. A glossary of technical terms would have much enhanced the value of the work to all but the professional systematic botanists.

THE ASPERGILLI.
By Charles Thom and Margaret B. Church.
The Williams & Wilkins Co.
$5.00 6 x 9; ix + 272 *Baltimore*

A detailed, systematic treatise on the fungi of the genus *Aspergillus*. The authors have found, and base their account upon, the original descriptions of all but three of the known species of this genus. In the case of these three they were compelled to rely upon secondary references. The work has been done with great care and the book will be a valuable addition to the shelves of every biological laboratory for, as the authors truly say, the *Aspergilli* are "the weeds of the culture room."

DIE ENTWICKLUNGSLINIEN DER KAKTEEN.
By Alwin Berger. *Gustav Fischer*
6 marks 6¾ x 10; iv + 105 (paper) *Jena*

A detailed, technical study of the phylogeny of the cacti. The book is abundantly illustrated with superb photographs beautifully reproduced. The author is of the opinion that the oldest cacti were tropical plants, and that early in their migration from the south into America they split into three main stem lines from which the present forms developed.

MORPHOLOGY

ÉTUDE MORPHOLOGIQUE ET MORPHOGÉNIQUE DU SQUELETTE DU BRAS ET DE L'AVANT-BRAS CHEZ LES PRIMATES. *Archives de Morphologie Générale et Expérimentale. Fascicule 24.*
By Ioan Gh. Botez. *Gaston Doin et Cie*
30 francs 6½ x 10; 174 (paper) *Paris*

This interesting monograph deals with the anatomy and development of the bones of the arm in the primates. Its point of view is that of modern physiological morphology. In particular, the author develops his evidence to show that, from the morphogenetic point of view, bone is not strictly a passive element fashioned by muscle as the active element, but on the contrary bone and muscle transform themselves simultaneously in their development in a relation of reciprocal dependence, in integration with the general state of organic equilibrium of the individual. There is a bibliography of 171 titles.

LA TÊTE. *Essai d'Anatomie Synthétique. Anatomie Médico-Chirurgicale. Anatomie des Formes Extérieures et Anatomie des Régions. Fascicule I. Le Crane. Fascicule II. La Face.*
By Philippe Bellocq *Masson et Cie*
25 francs (2 volumes) *Paris*
8¾ x 11; 260 (paper)

These volumes are based on the author's lectures in anatomy at Strasbourg, collected by Dr. Alfred Weiss, and edited and put in order for publication by Professor Bellocq. The first volume deals in detail with the anatomy of the skull and the meninges. It is illustrated with 36 figures, nearly all original and in the form of semi-diagrammatic line cuts. The second volume treats in the same way the anatomy of the face, with 46 illustrations. The volumes constitute a sound contribution to purely descriptive human anatomy.

PHYSIOLOGY

PRINCIPLES OF HUMAN PHYSIOLOGY.
By Ernest H. Starling. *Lea and Febiger*
$8.50 6¼ x 9¾; xiii + 1074 *Philadelphia*

There are extremely few men living today who could by any possibility give an adequate picture of the existing status of any large branch of science. Professor Starling modestly denies his ability to do this for physiology and graciously acknowledges aid from a number of his colleagues in the preparation of this fourth edition of his masterly textbook. But after making all due allowance for this help the reader cannot but stand aghast at Professor Starling's extraordinary genius for critically envisaging an enormous field of human knowledge. In conformity with a tendency manifest in a number of recent general physiological works, the amount of space devoted to biochemical matters has been reduced in this edition, which recognizes the development of a considerable degree of autonomy of this branch. The book will long continue to rank as one of the great standard reference works.

TROUBLES DES ÉCHANGES NUTRITIFS. *Physiologie, Pathologie, Thérapeutique. Tome I et II.*
By Ch. Achard. *Masson et Cie*
110 francs (2 volumes) *Paris*
6½ x 10; vi + 1220 (paper)

One cannot but admire the courage of a man who, in this day of rapid advance in biochemical knowledge, attempts unaided to write a 1220 page textbook on the

diseases of metabolism. The project was begun in 1912, was interrupted by the war, and has only now been brought to completion. Unfortunately, as Achard foresaw, no one man can cover such a large field, and even if he could, it would be impossible to get such a big book through the press in time to have it up to date. Furthermore, anyone, and perhaps particularly a Frenchman, is inclined to make such a work provincial by basing his views almost entirely upon the contributions of his own countrymen. Achard's book will serve as a mine of information for anyone who wants an *entrée* into the French literature on metabolism, but it will hardly satisfy an American who will find in it so little mention of what is commonplace on this side of the water. Even such a well known procedure as the phenolsulphonephthalein kidney function test is mentioned only in a short footnote; the blood and bile pigments are discussed without reference to the work of Whipple and his students, and Ambard's quotient is treated at length without reference to the extensive and careful work of Addis. There is a good index.

HANDBUCH DER PHYSIOLOGIE DER NIEDEREN SINNE. (*I. Band: Die Physiologie des Geruchs- und Geschmackssinnes.*)

By Emil von Skramlik. *Georg Thieme*
31.50 marks *Leipzig*
$6\frac{3}{4}$ x $10\frac{1}{4}$; viii + 532 (paper)

There has long been needed a comprehensive and critical review of the present state of knowledge of the physiology of the so-called lower senses (in contrast to sight and hearing). Zwaardemaker's valuable book on smell dates as far back as 1895. Doctor Skramlik, who is associate professor of physiology at Freiburg, proposes to fill this gap in the literature with the present treatise. This first volume deals with the senses of smell and taste. Two succeeding volumes will cover the senses of pressure (touch), heat, cold and pain. The volume before us is well done, carrying a sufficient amount of detail in the treatment, and yet achieving some degree of synthetic unity. Detailed references are given to the extensive literature. The book is well illustrated and thoroughly indexed.

HUMAN PHYSIOLOGY.

By John Thornton. Completely revised by William A. M. Smart.

Longmans, Green and Co.
$3.75 $5\frac{1}{2}$ x $8\frac{3}{4}$; vii + 463 *New York*

This third edition of a well-known quiz compend of human physiology has been thoroughly revised and in considerable part rewritten. By reason of its moderate size and the clear-cut manner of presentation it is not a bad resource for the general reader who wishes to get, without too much trouble, a reasonably comprehensive review of the present state of knowledge regarding human physiology. At the end there is a list of examination questions, partly original and partly selected from papers set in London examinations, followed by a glossary of technical terms and a detailed index. The book is extensively illustrated, mainly with borrowed cuts.

PHYSIOLOGICAL PAPERS. *Dedicated to Professor August Krogh.*

Wm. Heinemann (Medical Books) Ltd.
30 shillings *London*
$7\frac{1}{4}$ x $10\frac{1}{2}$; xvi + 375 (paper)

This *Festschrift* to the distinguished Danish physiologist contains twenty-two papers by Professor Krogh's former

students and associates, dealing with a wide range of physiological problems. The occasion which called forth the volume is a dual one; Professor Krogh's fiftieth birthday, and the removal from the old laboratory in Ny Vestergade to the new building erected for Professor Krogh's work through the munificence of the Rockefeller Foundation. The volume is beautifully printed and illustrated, with a fine portrait of Professor Krogh as frontispiece.

FOIE, PANCRÉAS, RATE.
By Dr. Mathieu de Fossey. *G. Doin et Cie*
10 francs $4\frac{3}{4}$ x $6\frac{1}{8}$; 164 (paper) *Paris*

A quiz compend on the diseases of the liver, pancreas, and spleen, with especial reference to methods of treatment and therapeutics.

BIOCHEMISTRY

DAS KOLLOIDE GOLD. (*Kolloidforschung in Einzeldarstellungen. Herausgegeben von R. Zsigmondy. Band 1.*)
By R. Zsigmondy and P. A. Thiessen.
Akademische Verlagsgesellschaft M. B. H.
Marks 7 6 x $8\frac{3}{4}$; x + 229 (paper) *Leipzig*

DAS KOLLOIDE GOLD IN BIOLOGIE UND MEDIZIN. *Die Goldsolreaktion im Liquor Cerebrospinalis.* (*Kolloidforschung in Einzeldarstellungen. Herausgegeben von R. Zsigmondy. Band 2.*)
By Ernst Joël.
Akademische Verlagsgesellschaft M. B. H.
6 marks 6 x $8\frac{3}{4}$; 115 (paper) *Leipzig*

These first two volumes in a new series under the general editorship of Professor Zsigmondy, are primarily of technical interest to the student of colloid chemistry, and to physiologists and clinicians interested in the application of the colloidal gold technique to diagnostic and similar biochemical reactions.

LEITFADEN DER KOLLOIDCHEMIE FÜR BIOLOGEN UND MEDIZINER. *Eine Einführung in die Allgemeine Physiologie, Pathologie, Pharmakologie.*
By Dr. Hans Handovsky. *Theodor Steinkopff*
12 marks *Dresden*
$6\frac{1}{4}$ x $9\frac{1}{4}$; xvi + 265 (paper)

The second edition of an introductory text-book of colloid chemistry, written especially from the point of view of the interests of biologists and medical men. It opens with a discussion of the general characteristics of disperse systems and the origin of such systems, followed by an account of the mechanical and electrical properties of disperse systems in general, and particularly colloid disperse systems. The last two sections of the book deal with the reactions of colloid systems and the structure and properties of gels. In an appendix there is discussed in an interesting general way the application of colloid chemistry to biological problems.

PROTEINS. *Lectures given in the United States of America in 1924.*
By S. P. L. Sørensen.
The Fleischmann Laboratories
$6\frac{1}{4}$ x $9\frac{1}{4}$; xx + 142 *New York*

This volume published by The Fleischmann Laboratories as a souvenir of the recent visit of Professor Sørensen to this country is useful, because it presents in convenient form the author's latest results and views regarding the chemistry of proteins. Besides the purely technical articles on proteins, there is an interesting chapter on the chemistry of bread making, with especial reference to the influence of hydrogen ion concentration. Unfortunately the book is not indexed.

SEX

Vacant

BIOMETRY

ZUWACHSRÜCKGANG UND WUCHSSTOCKUNGEN DER FICHTE IN DEN MITTLEREN UND UNTEREN HÖHENLAGEN DER SÄCHSISCHEN STAATSFORSTEN.

By Eilhard Wiedemann. *Walter Laux*

6¼ x 9¾; 190 (paper) *Tharandt, Germany*

This is a detailed biometric and general ecological investigation to determine the causes which are leading to the general damping off of the growth curve of the trees in the pine forests of Saxony. The broad conclusion is that the supposed laws of forest production do not have general validity, but the local situation must be taken into account in all cases because some peculiarity in it may markedly alter the growth curves. There is a bibliography of 169 titles. The study will be found of interest by ecologists as well as professional foresters.

PSYCHOLOGY AND BEHAVIOR

OUTLINE OF ABNORMAL PSYCHOLOGY.

By William McDougall.

Charles Scribner's Sons

$4.00 6 x 8¾; xvi + 572 *New York*

The author states that this volume is really to be considered as the second part of his well-known "Outline of Psychology." The two books taken together thus form a comprehensive treatise on the science of the mind in both its normal and pathological aspects. Professor McDougall's competence to deal with abnormal psychology is unusual, for he has had not only the purely scientific training and experience of the academic psychologist but also a medical training and extensive experience with clinical aspects of mental disorders. The result is a sounder and saner account than is to be found in much of the psychiatric writing of the present day. The general biologist, and particularly the student of animal behavior, will find the book especially useful in giving him a critical review of a field of study which is at once somewhat remote and recondite, but at the same time important to his own work.

TIERPSYCHOLOGIE. *Vom Standpunkte des Biologen.*

By Dr. Friedrich Hempelmann.

Akademische Verlagsgesellschaft M. B. H. M. 32 *Leipzig*

6¼ x 9½; viii + 676 (paper)

This is a thorough, critical and synthetic review of the literature of animal behavior. Somewhat more than half of the book—the special part—deals with the material on a taxonomic base, starting with protozoa and ending with vertebrates. The remainder of the book—the general part—discusses such general points as sensation, the brain as the organ of mind, the history and methodology of animal psychology, etc. There is an extensive bibliography covering 26 pages set in small type. The book is somewhat too sparsely illustrated, but contains excellent detailed indices. Altogether it is a treatise which every student of any aspect of animal behavior must have in his library.

LE DRESSAGE DU CHIEN DE CIRQUE.

By J. Dhers. *"Les Éditions de l'Éleveur"*

12 francs 4¾ x 7½; 85 (paper) *Paris*

This little treatise on the training of dogs for the circus and vaudeville stage,

by an "artist of the circus," will be found not only entertaining but of real and significant interest by the student of animal behavior and comparative psychology. It is a thoroughly practical treatise, written with characteristic French objectivity and precision. Everyone will be glad to know that the author's system of training grounds itself upon kindness, patience and understanding of the psychology of the dog, rather than upon fear, punishment, and cruelty. We commend the book highly to biologists, as well as to the trouper.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

NATURE'S ALCHEMY. *Special Bulletin of the Turck Foundation for Biological Research, etc.*
The Turck Foundation for Biological Research
—— 8½ x 11; 62. *New York*

This entertaining volume tells all about Dr. Fenton B. Turck, The Turck Foundation for Biological Research, cytost, and anti-cytost. It was prepared under the supervising editorship of Mr. Hamlin Garland, 507 Cathedral Parkway, New York City, from whom biologists can probably obtain free copies. The following quotations will perhaps indicate the desirability of so doing:

"That cells cannot automatically perform the functions of growth, that they must be stimulated to action, is established. That each cell holds within itself a 'self-starter' is also agreed upon. This substance has been variously named 'cell-sap,' 'tissue extract,' and the like. LaMarck (*sic*) called it 'that subtle fluid,' but Turck named it 'cytost' from the Greek word cytos, meaning cell.

"For more than thirty years Turck has been experimenting with this 'activating principle,' one of the most powerful and mysterious elements in nature, and it is upon the character and action of 'cytost' that his activities are still concentrated.

" . . . . From a long series of experiments in his laboratory he demonstrated that many disorders in animal tissue were due to abnormal cell breakdown and the liberation of excessive quantities of cytost into the cell media. Just as excess of cytost in the soil is the cause of disease in plant tissue, so excess of animal cytost in the fluids surrounding the cell produces disease and death in animals.

"He demonstrated as many others from LaMarck (*sic*) to Conklin had done, that the cell contained its own activating element, but he went further. 'No matter what the agent which liberates this element may be,' he says, 'we have shown that in certain measured concentrations cytost stimulates the growth of tissue, in larger amounts it destroys tissue.'

"Absolutely necessary to the cell in dilute proportions, it is in excess injurious to the cell. Like electricity, it is stimulating when acting as a light charge, but acts as a disrupting force in case of high power.

"Turck demonstrated other and still more marvellous properties in this element. He found by actual experiment that it was *specific to the species*, that is to say, cytost obtained from the tissues of a cat's heart was different in quality and action from cytost extracted from the tissues of a dog's heart. In the one case the cytost carries a charge of 'cat' and in the other a charge of 'dog.' . . . .

"From a study of the varying degrees of resistance to the action of cytost on the part of different animals, it was but a short step to the production of immunity. Reasoning that there must be a counterbalancing element in the blood of the immunized animal, Turck carried out experiments which not only raised the

animal's resistance to disease to a very high degree but led to the isolation of the opposing element.

"Injecting cytost made from human tissue into a horse at intervals over several months' time, he demonstrated that the animal had built up in its blood a substance which strongly tended to offset the toxin action of the cytost, for when a portion of the animal's blood was drawn, dried and *burnt to an ash* there remained in the mineral salts of this ash, an element which proved to be the *negative* charge as cytost was the *positive* charge of the life force.

"This counter-balancing substance which he thus isolated and used in creating a higher degree of resistance to disease in the human organism he very naturally named Anti-cytost.

"Having in his possession and under his control both of these subtle elements, he was able to produce in this laboratory by their use in action and re-action, both active and passive immunity in animals. After hundreds of experiments with these opposing substances he came to the momentous conclusion that *health is a dynamic or continuing equilibrium between them* and that the cell is the meeting point of two all-pervasive life forces, a minute stage on which these positive and negative powers strive for the mastery.

"The man of science cannot use the word 'marvellous' but we as laymen permit ourselves to wonder at the patience and skill with which Turck has brought his conception to a concrete demonstration.

"In many of his experiments, Turck has found the germ a 'secondary invader.' Germs of one kind or another are always present in the organism but appear to have no potency until a break in the tissue occurs.

"In the *Medical Record*, May, 1919, Turck makes report of various experiments in which he sprayed into the nostrils and throats of cats, varying quantities of pneumonia organisms, causing no pneumonia, but when he mixed cytost with these germs, pneumonia at once developed. He produced pneumonia at will by the use of lung-tissue autolyzed under sterile conditions. By spraying, by injection and by covering the paws of animals with a paste of lung-tissue he obtained typical pneumonitis.

"Another and equally significant experiment involved the gathering and burning of the dust of the room in which cytost had been produced and in which various demonstrations had taken place. Upon reducing this dust to an ash, and adding a portion of sterile water, Turck obtained sufficient cytost to kill a cat.

"This experiment with the dust of the room burned to an ash, suggests that the over-crowding which leads to disease in tenements, is not solely a question of germ infection, but also of the presence of cast-off cell debris.

"There are still wider reaches to Turck's experimentation. Extending his interest to the parent cell, he proceeded to demonstrate that the size, weight, vitality and fecundity of animals could be affected by the graduated use of cytost.

"Taking flocks of fowls, litters of kittens and rabbits, he separated them into groups, some to be held as normal 'controls' while the others were being treated by injection of cytost. The treated animals outgrew their fellows, were more active, lived longer, and were more fecund.

"Furthermore, he found that he could not only build a larger and finer animal organism by the use of cytost, but that the increased hardihood, the larger size, the finer fur, and other individual excellencies of the parents were transmitted to the offspring. He was able not only to

stimulate the growth of guinea pigs and cats, but to lengthen the life of succeeding generations. Laboratory animals of the third and fourth generation continue to show the benefits transmitted to them.

"The results of these experiments have been tabulated and published in various medical and surgical journals. His protocols show that the laying power of hens has been increased by the use of this natural cell stimulant, and that the fur of cats and guinea pigs was made richer and glossier, all evidences of increased vitality."

In spite of the prohibition quoted above we think that every man of science will yield to the overwhelming temptation and say MARVELLOUS!

HAVELOCK ELLIS. *A Biographical and Critical Survey.*
By Isaac Goldberg *Simon and Schuster*
$4.00 5¾ x 8¼; xiv + 359 *New York*

The author has not succeeded so well in the application of his somewhat novel biographical technique to Havelock Ellis as he did in his first essay in that direction, with H. L. Mencken as the subject. After finishing the volume the reader is still not satisfied that he knows very much about the real Havelock Ellis. There is a great deal in the book about Mrs. Ellis and her writings. The emphasis throughout is on the literary side of Ellis' character and work. What makes the volume particularly disappointing to the biologist is the inadequacy of the discussion of his scientific work. However, it must be said that the book taken as a whole gives a more informing picture of a great contemporary than anything else now available. It is less extensively and less significantly illustrated than was the Mencken volume.

ENSEIGNEMENTS NATURISTES
By Dr. Paul Carton *Norbert Maloine*
15 francs 4¾ x 7½; 384 (paper) *Paris*

A fine piece of quackery proving conclusively that, even with Abrams to our credit, we have no monopoly of the breed in this country. A "naturist" is a person who is against good food, good drink, good tobacco, and most of the other achievements of pleasant living. Raw vegetable foods are the key to health, wealth, and happiness. Those who find enjoyment in the contemplation of the manifestations of the outlying aberrations of the human intellect will be entertained by this volume.

THE COST OF BIOLOGICAL BOOKS IN 1926

By RAYMOND PEARL

During the first year of the existence of The Quarterly Review of Biology there have been noticed in the department devoted to *New Biological Books* somewhere in the neighborhood of 300 separate books. I have been interested to note the considerable variation in their prices, as they have come in to the editorial office. This has led me to prepare a brief summary of the situation as it has developed during the year 1926. It is proposed to make such a *résumé* of the book price situation an annual feature.

I have first of all classified the books which have been reviewed in our pages according to the country of publication, under the following rubrics:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of the books reviewed during the year have had this origin.

II. *Germany.* In the number of books sent in by publishers for review Germany stands next to this country. There has grown during the year a strong feeling in the editorial office that German publishers of scientific books, as a class, are distinctly more wide-awake and enterprising in their attempts to secure a world-wide distribution of their product than are the corresponding groups in other European countries.

III. *English-American.* In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other Countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.* In any discussion of book prices it would be manifestly unfair to include government publications with the product of American commercial publishers.

In the table which follows there are given, for each of the sources of origin listed above, the following items:

a. Total number of pages in the books which have been reviewed in Volume I of The Quarterly Review of Biology, *excluding* those books which either had no price, because they were intended for free distribution, or because we were unable to find out, after diligent inquiry, what the price was. Anyone who has had no experience of the matter would be amazed at the number of books which are distributed by their publishers without any indication whatever, on either book or wrapper, as to what it is proposed to charge for them. Not infrequently it takes two or more letters to extract this information from a reluctant publisher. Just why they are so set on keeping the matter secret is impossible to say.

b. The total cost, in dollars, of those books having their total pages given in the first column. In computing these values for books originally priced in a foreign currency I have used the exchange

rates prevailing at the time the book was received. These prices then represent fairly what an American biologist would have had to pay if he had bought these books at the time they came to us.

c. By the simple process of dividing the figures in the second, or *b* column, by those in the first, or *a* column, we arrive at those in the last column, which therefore give the average *price per page* of the aggregate of books received from the several sources. By judicious attention to the location of the decimal points these prices in the last column of the table are exhibited as so many *cents per page*.

Prices of Biological Books, 1926

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
English-American	7,938	$122.65	1.55
Other countries	1,799	27.13	1.51
England	5,423	69.48	1.28
United States	43,049	480.87	1.12
Germany	16,431	179.23	1.09
France	5,306	18.42	0.35
U. S. Government	2,629	8.25	0.31

On the basis of cents per page it appears from the table that the books emanating from the American branches of English publishing houses have been the most expensive during the past year, so far at least as may be judged from these samples. The next most expensive, as a class, are those published in the "Other Countries" not separately specified. Then follow the English books, and then those published in the United States. At about the same level, but actually 0.03 of a cent lower per page, come the German books. The only cheaper class of commercially published books are the French, which have had the lowest price of all such, costing only slightly more per page than the United States Government publications.

In interpreting these results certain outstanding factors need to be kept in mind. In the first place the English-American have had to pay duty to enter the United States, and the prices here quoted for these books include the duty. There is presented here to the American biologist a concrete illustration of the meaning to him of protecting infant industries. There are those who have contended, and spent much of their personal time and energy in a vain endeavor to convince our legislators, that the taxation of intellectual progress was neither good business nor exactly sporting. But some of the American publishers and about all the printers think otherwise, and they speak a language more easily understood by our lawgivers.

In the case of books listed under the heads "England" and "Other countries" (so far as the latter are in the English language) the prices do *not* include duty. But the American biologist would have to pay duty, and therefore the price to him would be even higher than the table shows.

There is a widely prevailing impression that the German publishers are greatly over-pricing their products at the present time. This does not seem to be the case, so far as the present sample of new biological books is concerned. Making due allowance for the fact that the majority of the German prices included in the table are for books in paper covers, it turns out that the biological books received from Germany during 1926 cost almost exactly the same per page as those turned out by American publishers. And any American publisher can prove that he is selling his books at just as low a price as he can afford to and escape bankruptcy proceedings. Perhaps German books ought to sell lower than those published here, because of generally lower labor costs in Germany,

but there are other complicating economic factors which enter the case.

Of all places in the world during 1926 France has been the spot of choice to buy books. French publishers have signally failed to adjust their prices correctly to the degree of emaciation of the franc. What will happen in the future a mere biologist cannot predict. But there is a possibility, at least, that presently the French publishers will over-compensate in this matter, as the Germans are alleged to have done when their currency became stabilized, and put their prices as much too high as they have been too low in 1926.

Finally there must be a word of appreciation of the boon which the Government Printing Office is to American scientific men. It regularly publishes memoirs of the first importance and distributes them at a price which makes them available to even a beginning instructor.

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